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Reactor for Determination of Dimethyl-β-Propiothetin in Tissue of Marine Origin by Gas–Liquid Chromatography[1]

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ABSTRACT

Dimethyl-β-propiothetin is found in a number of marine plants and may accumulate in fish. The decomposition of this material by cold concentrated alkali, yielding dimethyl sulphide, is believed to be a specific reaction. A versatile reactor system, suitable for the production of such volatile materials, is described. Coupling of this reactor system to a gas–liquid chromatograph employing a flame ionization detector permits rapid and quantitative estimation of the dimethyl-β-propiothetin present in fish tissues through determination of the dimethyl sulphide.

INTRODUCTION

Dimethyl-2-carboxyethyl sulfonium chloride (or dimethyl-β-propiothetin (DMPT)) is found in a number of marine plants (reviewed by Challenger, 1959a) and consequently may pass through the food chain from phytoplankton through zooplankton to accumulate in commercially valuable species of fish such as chum salmon (Motohiro, 1962). Spontaneous decomposition yielding dimethyl sulphide (DMS) may occur on the death of at least some plants (Challenger, 1959b), although DMPT is not decomposed by the digestive juices of chum salmon (Motohiro, 1962a). The objectionable DMS found in cod from the Labrador area (Sipos and Ackman, 1964) presumably originates from DMPT in the first instance although this has not been proven, and it is not known if the DMS is liberated after ingestion of the algae by the zooplankton or at another point in the food chain.

The original and subsequent analyses of marine organisms and certain other plants for DMPT have involved extraction, concentration, and precipitation steps (Challenger, 1959c; Motohiro, 1962b). These required fairly large amounts of sample and were considered unsuitable for processing large numbers of samples in a projected investigation of the deposition of DMPT in cod. The facile liberation of DMS from DMPT by concentrated cold alkali (Challenger, 1959d) was demonstrated by a simple gas–liquid chromatographic head-space procedure (Sipos and Ackman, 1964). This preliminary experiment also showed that the sensitivity was adequate for the proposed investigation and that other volatile constituents from fish apparently did not interfere. To place the experiments on a quantitative basis a reactor system coupled directly to the gas–liquid chromatograph was constructed as described below and found satisfactory.

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REACTION APPARATUS

The apparatus developed for the release of DMS in DMPT determination is depicted schematically in Fig. 1 and illustrated in Fig. 2. The basic requirements, other than a suitable valving arrangement for injection of the volatile reaction products into the gas–liquid chromatograph, were for a rapid means of changing inexpensive sample containers and provision for the injection of appropriate reagents. Glass vials taking a GCMI 24-mm cap (Kimble Glass Co.) were available in a number of sizes and the same thread was also found in some larger bottles. The dimensions of the unit were thus basically determined by the size of the Teflon[2] piece with female thread and associated body post (Fig. 1). The latter was intended to reduce the dead volume and distribute the carrier gas for rapid and even sweep-out of the gas space. The lower body post dimension of $\frac{9}{16}$-inch diameter passed readily into all the vials tried but required a slight expansion to conform to the Edwards Elastomer vacuum "0" ring No. VOR 120. The gas inlet ports, shown in cross-section in Fig. 1, actually numbered three, arranged radially as permitted by the vertical borings to ensure even sweep-out of the gas space. The injection port hole ($\frac{1}{16}$-inch ID) was expanded at the top to $\frac{7}{32}$-inch. The silicone rubber injection septums furnished for the glass columns of the Barber-Colman Model 10 gas chromatograph satisfactorily resisted pressures of up to 40 psig when fitted in this

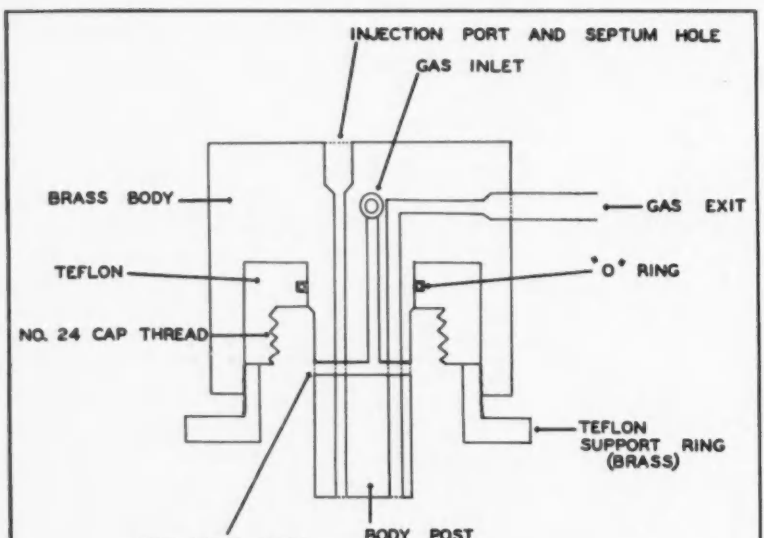

FIG. 1. Schematic cross-section of reactor for the decomposition of DMPT and injection of liberated DMS into gas–liquid chromatograph.

[2]DuPont registered trade mark.

hole. Copper tubing ($\frac{1}{8}$-inch OD) soldered directly into the body of the reactor passed gas in and out via connection to the manifold of the injection valve (Fig. 2).

The Wilkens 6-Way gas sampling valve[3] and two toggle valves completed the gas flow system. Opening toggle valve No. 1 permitted carrier gas to flow from a T connection in the carrier gas line into the reactor and opening toggle valve No. 2 permitted escape to the atmosphere for purging and pressurizing the reactor system without disturbing the gas–liquid chromatographic column.

The gas–liquid chromatographic column was connected via $\frac{1}{16}$-inch OD stainless steel tubing and a Swagelok[4] connector directly from the outlet of the 6-Way gas sampling valve and was of stainless steel tubing, 6 ft long and $\frac{1}{8}$-inch OD, packed with 20% Tween 80 on 80–100-mesh Chromosorb W. At 30 psig the flow rate was 100 ml/min. Although mounted in an oven without applied heat, the operating temperature was normally in the range of 28–30 C owing to the heat from the base of the Wilkens Hi-Fy type flame ionization detector. A circulating fan was operated in the oven to keep the air from stratifying. The flame ionization detector was connected to a Wilkens Model 500 electrometer and Minneapolis-Honeywell 1-mv recorder fitted with a Disc Instruments, Inc., ball and disc-type integrator. Owing to the very high carrier gas flow rate it was necessary to employ air and hydrogen flow rates somewhat higher than recommended for this detector, but baseline stability and noise level were excellent at 2X electrometer sensitivity.

The glass vials actually employed were 27 mm OD and 58 mm long. A large number was sorted on the basis of easy threading into the Teflon female thread. The lips of selected vials were then lightly ground with medium carborundum powder. This served the double function of flattening slight imperfections and of providing a gripping surface to hold the vials against the Teflon. If not ground the vials usually promptly unscrewed themselves. Finally the vials were pressure- and leak-tested in the reactor by submergence in water while pressurizing to 35 psig.

Injections of reagents were effected with conventional hypodermic syringes or Becton-Dickenson Luer-Lok syringes, with 2-inch 25-gauge Huber point needles. Hermetically sealed Teflon-covered stirring bars were employed. Owing to the small size a powerful magnet in immediate proximity was necessary to stir blended fish flesh. The stirrer (Fig. 2) was pivoted on a bench mount to swing directly under the vial after insertion in the reactor.

OPERATION VARIABLES AND RESULTS

Only a limited study of variables was carried out to establish suitable operating conditions. The effect of time on the reaction was determined by two procedures and linear relationships were found for the response of the DMS peak from standard aqueous solutions of DMPT (Fig. 3). In the first

[3]Wilkens Instrument and Research Inc., Walnut Creek, California.
[4]Crawford Fitting Co. registered trade mark.

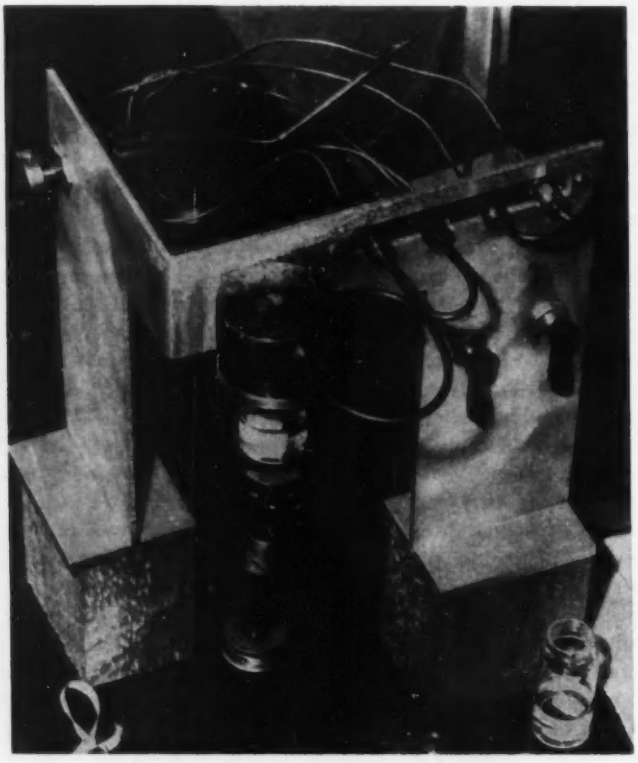

FIG. 2. Reaction apparatus with associated valves and tubing connections (including connection to gas–liquid chromatograph), showing vial and magnetic stirrer in position.

method (lines A and B) the procedure involved injection of DMPT solution (1 ml) into 7.5 N sodium hydroxide solution (7 ml), the vial being first pressurized via toggle valve No. 1. After the appropriate time the gas-sampling valve was depressed for 5 sec (by stopwatch) to inject the liberated DMS into the gas–liquid chromatographic column. The 5-sec time interval provided ample carrier gas to sweep out the reactor space and gave peaks of adequate sharpness on the gas–liquid chromatograms and was also a sufficient time interval to permit reproducible hand operation. In this procedure the continuance of stirring during the injection period gave a small but reproducible additional yield of DMS. Subsequently this procedure was found unsatisfactory with fish flesh blends since fibres and particles of tissue either jammed the syringe barrel or plugged the needle. Clarified liquids could however be analysed by this procedure.

In the second procedure, finally adopted for laboratory use as simpler for sample preparation, the NaOH (1 ml) was injected into the solution of

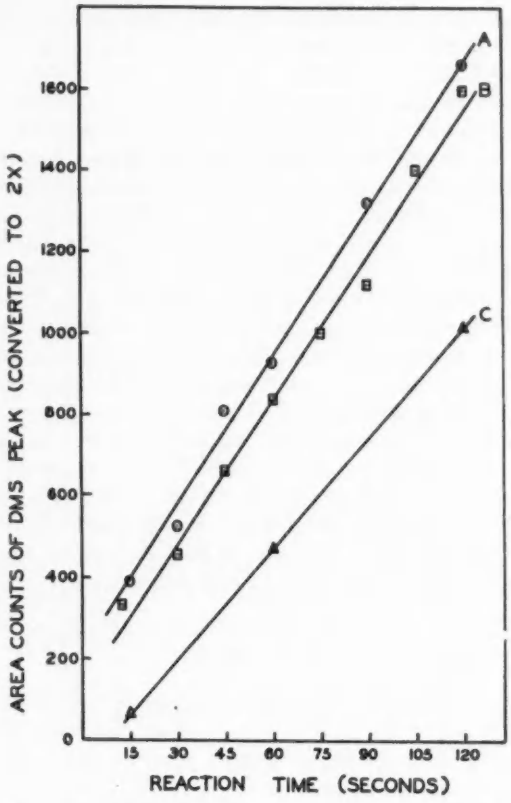

FIG. 3. Effect of time on yield of DMS as determined by gas–liquid chromatography. A: 0.01% DMPT solution (1 ml) injected into vial containing 7.5 N NaOH (7 ml) with stirring during DMS injection. B: as in A without stirring during DMS injection. C: 7.5 N NaOH (1 ml) injected into vial containing 0.01% DMPT solution (1 ml) and water (6 ml), with stirring continued during DMS injection.

DMPT with stirring after preliminary sweep-out and pressurization of the vial. The volume of DMPT solution was arbitrarily set at 7 ml to provide a reasonable amount of material without risk of the liquid touching the body post and being carried into the gas chromatographic system. The yield of DMS was again found to be linear with time (Fig. 3, line C). Owing to difficulty in reproducing the high gas flow rates the actual response of the detector varied appreciably from day to day but was always consistent for any set of conditions. Multiple standard samples were run at the beginning of each day's operation and a single one as a check at the termination of the work. With experience an operator readily attained results reproducible to better

than 5% in consecutive analyses of the same DMPT solution. The slightly different results for the two procedures are therefore probably partly due to detector response in addition to the effect of procedure. Injection of concentrated alkali solutions is entirely feasible against 30 psig but a face shield or goggles should be worn to protect against possible accident.

The reaction time of 2 min under either procedure gave an adequate sensitivity for the purpose intended since solutions as weak as 0.0001% in DMPT gave ample DMS for detection and measurement. In a further experiment, using the 2-min reaction time and the second analytical procedure outlined above, the yield of DMS as measured on the gas–liquid chromatograph was shown to be proportional to the DMPT present (Fig. 4). The range of concentrations covered in this experiment correspond to those anticipated and found in feeding experiments with cod (Ackman and Dale, unpublished).

The following materials were investigated by the second procedure, in amounts exceeding those anticipated in fish blends, and were found to give either no gas–liquid chromatographic peaks or minor peaks not interfering with the DMS determination: amino acids (L-cysteine hydrochloride, DL-methionine, L-arginine hydrochloride, L-cystine, and DL-homocystine), fish flour (for amino acid analysis see Guttman and Vandenheuvel, 1957), cod flesh, cod liver, cod stomachs, herring flesh, and herring viscera. The cod specimens were obtained live at Terence Bay between August and December

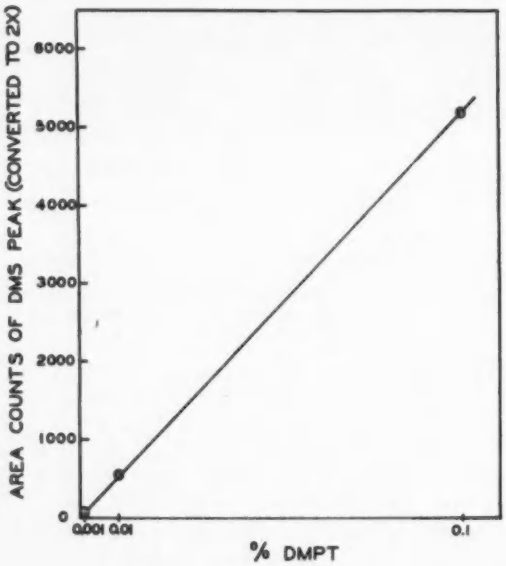

FIG. 4. Recorder response for gas–liquid chromatographic estimation of DMS from DMPT solutions of varying concentrations. Conditions as in Fig. 3(C) with 2-min time of reaction.

1964 and held for several weeks before being killed. The herring were obtained frozen from a local supplier (origin not known) and were fed to the above cod during live holding.

At the sensitivities employed with the flame ionization detector, contamination of the samples with volatile materials not naturally present could present problems, although on only one occasion did an unexplained peak appear in the vicinity of the DMS peak. The use of solvents near fish dissection (in poorly ventilated low temperature laboratories) and near the gas chromatograph did give additional peaks on the gas–liquid chromatograph. The presence of DMS in materials such as cod flesh does not hinder DMPT determinations, since the DMS (bp 38 C) may be rapidly removed from a blended slurry of cod flesh on a rotary evaporator at room temperature under water aspirator vacuum. Provided the temperature does not exceed 50 C (Motohiro, 1962c) the same process may be used to concentrate DMPT solutions tenfold with 85–95% recovery of DMPT (Ackman and Dale, unpublished).

DISCUSSION

The reaction of DMPT with cold concentrated alkali to give DMS appears to be a specific test. Salts of α-thetins may give DMS on heating with water or acid (Challenger, 1959e), and some sulphonium compounds in marine algae and in other plants give DMS on boiling with alkali (Challenger, 1959f). The other products of the breakdown of DMPT by alkali are acidic (Challenger, 1959g; Motohiro, 1962d) and hence not volatile in the presence of alkali.

The sensitivity of the reactor gas–liquid chromatographic method is very good. In the present experiments 0.0001% DMPT in cod flesh blended with water (1:4) was readily detected *without concentration steps* and on only 7 ml of blended sample. The gravimetric method as employed by Motohiro (1962e) is shown to detect 0.00001% DMPT but this is based on concentration from a much larger sample.

In the analysis of materials such as food volatiles the number of systems for trapping and subsequent injection of volatiles into gas–liquid chromatographic apparatus is too large to be reviewed (Hornstein and Crowe, 1964). With the introduction of the more sensitive ionization detectors the use of head space techniques (Buttery and Teranishi, 1961, 1963; Kepner *et al.*, 1964; Bassette *et al.*, 1962) has become popular since in many cases more representative proportions of volatiles may be obtained by this technique than by trapping. The volatiles may be reliably quantitated by such procedures (Ozeris and Bassette, 1963; Kepner *et al.*, 1964). In most of these instances, as in the determination of DMPT, water as a solvent is of no significance since the flame ionization detector does not respond to water. Water must be avoided with argon ionization detectors (Self *et al.*, 1963a, b). When using either type of detector for specific chemical reactions, relatively nonvolatile solvents such as glycols or the higher hydrocarbons might be used in some cases, while with commonly used solvents such as alcohols of moderate vola-

tility either programmed temperature gas–liquid chromatography (Buttery and Teranishi, 1963; Teranishi *et. al.*, 1962; Hornstein and Crowe 1962) or column backflushing could be employed to clear the column after each reaction if necessary.

In some commercially available gas chromatographic units operating on a reactor principle, such as the Fisher Clinical Gas Partitioner, the head space sampling technique is not used. Instead, carrier gas is bubbled through the reaction mixture to sweep out the desired volatile materials or gasses. Such equipment might be used for the analysis of DMPT if modified with proper columns. It is probable that a suitable ionization detector would have to be installed to attain desirable levels of sensitivity.

Sub-ambient temperature column operation (Merritt and Walsh, 1963) could be advantageously employed in instances where very volatile reaction products with short retention times would be produced. This is particularly possible since a high carrier gas flow rate appears necessary to sweep out the reaction vessel. Optional attachments to the apparatus as described might include the attachment at toggle valve No. 2 of a manometric system if desired or of a vacuum where necessary. In the analysis of DMPT the latter could be used for removal of DMS or other volatiles with the sample *in situ*.

A number of somewhat similar valve arrangements has been described, particularly for injections of trapped samples into gas–liquid chromatographic columns (Bellar *et al.*, 1963). Limited use could perhaps be made of the present apparatus in this type of work. However it is particularly suited for reactions where volatiles are liberated, and for example might have application (although not with a flame ionization detector) in the determination of carbon dioxide in sea water (Park *et al.*, 1964). Subtractive procedures for identifying volatile materials could also be employed (Bassette *et al.*, 1962; Hoff and Feit, 1964).

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Activity Coefficient of the Sodium Ion in Sea Water[1]

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ABSTRACT

The activity coefficient of the sodium ion in sea water has been measured by means of a sodium ion glass electrode. The activity coefficient was 0.68 at 25 C and 35‰ salinity and increased with decreasing concentration and decreasing temperature.

INTRODUCTION

Glass electrodes which are sensitive to cations other than the hydrogen ion have been in use for some years (e.g. Eisenman *et al.*, 1957). One such electrode, developed by Beckman Instruments, Inc., has good sensitivity for sodium ions in sea water and suffers very little interference from other ions present. A similar electrode has been used by Garrels and Thompson (1962) to measure the "sodium ion activity" in sea water $(a_{Na^+})_{sw} = (\gamma_{Na^+} m_{Na^+})_{sw}$ where γ_{Na^+} is the sodium ion activity coefficient and m_{Na^+} is the molality of the sodium ion. In spite of the common usage of individual activity coefficients they have limited thermodynamic significance since any electrode system must involve either the mean activity coefficient of a cation and an anion or an unknown liquid junction potential (Guggenheim, 1929). However, Shedlovsky *et al.* (1963) use the term *p*Na to refer to sodium ion activities determined with these electrodes, and Rechnitz and Zamochnik (1964) give a useful potential comparison method for calibrating these electrodes which also was used in the present work.

EXPERIMENTAL PROCEDURE

All measurements were made with two pairs of Beckman 39278 sodium ion electrodes and Radiometer K100 calomel electrodes with saturated KCl salt bridges. The EMF generated by each electrode pair was measured to ± 0.1 mv with a Radiometer 4 pH meter. The electrodes were calibrated with solutions of NaCl of known molality for which it was assumed γ_{Na^+} was given by the mean activity coefficients of NaCl ($\gamma \pm$) given by Robinson (1939) as a function of concentration and temperature. The temperature of the solutions was kept at 25 C unless otherwise stated.

No significant difference in EMF was given by solutions prepared from freshly opened A.R. grade NaCl or from NaCl that had been precipitated with HCl and fused at red heat in a platinum dish. The sea water used in the

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investigation was obtained from the IAPO Standard Sea-Water Service, Denmark, and had a salinity of 35‰. Lower salinities were obtained by dilution with distilled water. The molality of the sodium ion in the sea water was calculated from the tables of Barnes (1959).

The electrodes were stored in 1 M NaCl. Measurements were made after rinsing the electrodes with distilled water, immersing them in the test solution, and flushing each bridge with a drop of KCl (several flushings resulted in negligible contamination of the solution by KCl). Readings on each electrode pair were made alternately and readings were accepted when they could be repeated within 0.5 mv. Because of differences in asymmetry potentials of the glass electrodes the readings for each electrode pair differed by several tens of millivolts. The effect of electrode drifting was minimized by making measurements with progressively increasing and then decreasing concentrations of NaCl and by straddling seawater measurements with measurements of NaCl solutions of both higher and lower $(m_{Na^+})_{NaCl}$ than that in sea water. After a plot of EMF vs $(m_{NaCl}\ \gamma\pm)$ had been made, the values of EMF for the seawater samples for that run were converted to $(a_{Na^+})_{sw}$ by interpolation from the plot. The value of $(\gamma_{Na^+})_{sw}$ was then given by $(a_{Na^+}/m_{Na^+})_{sw}$. The results of a typical run are shown in Fig. 1. Each curve represents the results of one electrode pair.

It was assumed that the liquid junction potential between the test solution and the KCl bridge was the same in the NaCl solutions as in the sea water so that no correction was necessary for this potential.

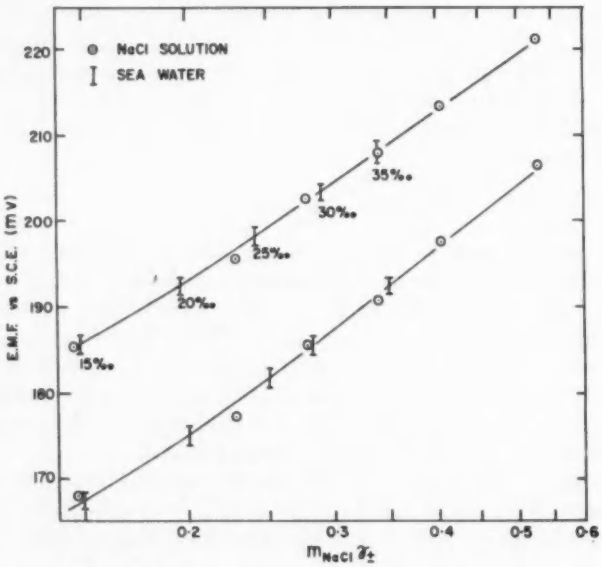

FIG. 1. Effect of NaCl activity on EMF generated by glass electrode-calomel electrode pairs.

RESULTS

The effect of possible interfering ions on the electrodes was measured by adding the following salts, in the concentrations normally present in sea water (Goldberg, 1961) to NaCl solutions: $MgCl_2$, $CaCl_2$, KCl, and $AgNO_3$. Each salt lowered γ_{Na^+} by an amount expected from the increase in ionic strength[2] due to adding the salt. The hydrogen ion is without effect above pH 6.

Replacement of the glass electrode with a sodium amalgam electrode (also specific for sodium ions) gave the same value for $(\gamma_{Na^+})_{sw}$ as did the glass electrode.

The effect of salinity of sea water on $(\gamma_{Na^+})_{sw}$ is shown in Table I and in Fig. 2, and the effect of temperature on $(\gamma_{Na^+})_{sw}$ is shown in Table I and in Fig. 3. Each result is the mean of at least three pairs of determinations and is shown along with its standard deviation. Garrels and Thompson's (1962) value for $(\gamma_{Na^+})_{sw}$ is shown for comparison in Table I and in Fig. 2. In addition, the mean activity coefficient of NaCl, and values for γ_{Na^+} calculated by Kielland (1937) are shown for the same ionic strength as that of sea water.

CONCLUSIONS

The activity coefficient of the sodium ion increased with increasing dilution of the sea water and was consistent, within experimental error, with

TABLE I. The activity coefficient of Na^+ in sea water as a function of salinity and temperature.

	T = 25 C.			Salinity = 35‰ μ = 0.72		
Salinity (‰)	$(\gamma_{Na^+})_{sw}$	μ	$\gamma\pm$[a]	Temperature (C)	$(\gamma_{Na^+})_{sw}$	$\gamma\pm$[a]
35	0.68±0.014	0.72	0.665	45	0.66±0.014	0.666
30	0.68±0.02	0.62	0.671	35	0.68 "	0.667
25	0.69 "	0.52	0.679	25	0.68 "	0.665
20	0.71 "	0.41	0.692	25	0.76[c] –	–
15	0.72 "	0.31	0.708	15	0.69±0.014	0.664
10	0.71 "	0.20	0.735	5	0.70 "	0.660
5	0.75 "	0.10	0.778			
–	0.77[b]	0.10				

[a]Values of Robinson (1939) for NaCl solutions of same ionic strength as sea water.
[b]Kielland's (1937) value for γ_{Na^+} in NaCl solution.
[c]Garrels and Thompson's (1962) value.

[2]The ionic strength is defined as $\mu = \frac{1}{2} \Sigma m_i z_i^2$, where m_i is the molality of ion i and z_i is its charge.

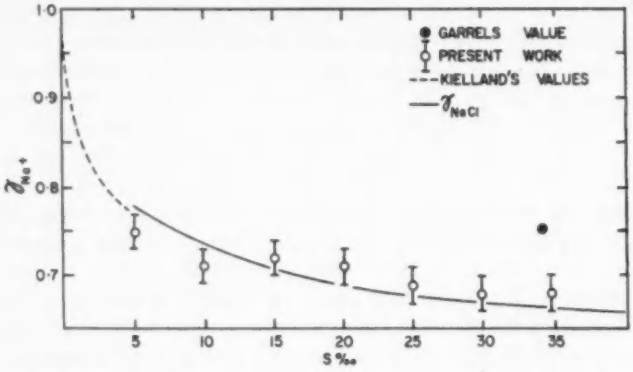

FIG. 2. Effect of salinity on sodium ion activity in sea water at 25 C.

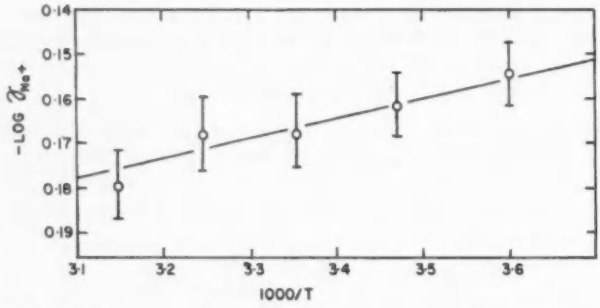

FIG. 3. Effect of temperature on sodium ion activity in sea water at 35‰ salinity.

the activity coefficient of either NaCl or Na^+ of the same ionic strength as the sea water at 25 C. A significant difference was found between the value of $(\gamma_{Na^+})_{sw}$ reported by Garrels and Thompson (1962) and that found here. Garrels and Thompson calibrated their electrodes at low ionic strengths and extrapolated these calibrations to higher ionic strengths, although it was concluded from the present work that due to nonideal behaviour of the electrode such extrapolation would have given values of $(\gamma_{Na^+})_{sw}$ which were in error.

The partial molal heat content, $\bar{L}$, of a salt in solution can be calculated from the temperature coefficient of the mean activity coefficient (Harned and Owen, 1958):

$$\frac{\delta \ ln \ \gamma \pm}{\delta \ (1/T)} = \frac{\bar{L}}{\nu R}$$

where ν is the number of ions produced by the dissociation of one molecule of the salt and R is the gas constant. The value published in the literature

for $\bar{L}$ for 0.7 M aqueous sodium chloride at 25 C is −130 cal/mole (Robinson, 1939). Assuming that values for $\bar{L}$ apply to single ions we can calculate from Fig. 3 that $\bar{L}_{Na^+}$ is about 200 cal/mole. If ionic heat contents are additive this implies that $\bar{L}_{Cl^-}$ should be large and negative in sea water. It is reasonable to expect the NaCl in sea water to behave similarly to the NaCl in pure solutions since NaCl contributes over 70% to the total ionic strength of sea water. However, because of the difference in temperature coefficients between $(\gamma_{Na^+})_{sw}$ and γ_{NaCl} this similarity exists only at about 25 C.

While the results presented here involve the assumption that the change of liquid junction potential of the reference electrode on going from sea water to NaCl is negligible, they do provide a guide to the behaviour of singly-charged cations in sea water. The agreement with the value $\gamma\pm$ for NaCl at 25 C suggests some justification for the present practice of assuming that the activity coefficients of ions in sea water can be given by the mean activity coefficient of ions of a salt solution having the same ionic strength as the sea water. This approximation will be less valid for the less abundant ions in sea water. Furthermore, the good agreement observed in the present work is to some extent fortuitous in view of the complexity of ionic interactions in concentrated solutions of mixed electrolytes Even extensions of the Debye-Hückel theory allowing for hydration effects are unsatisfactory for the treatment of such solutions (Robinson and Stokes, 1959).

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Ketone Bodies in the Blood of Salmonoid Fishes[1]

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ABSTRACT

The concentration of acetoacetate expressed as acetone in the blood of rainbow trout (*Salmo gairdnerii*) was generally in the range of 0.3–1.0 mg/100 ml and long periods of starvation did not appear to affect this level to any appreciable extent. In sockeye salmon (*Oncorhynchus nerka*) in the pre-spawning stage of migration the concentration of acetoacetate was within the range found for rainbow trout. Higher concentrations of acetoacetate, amounting to approximately 1.5 mg/100 ml of blood, were present in sockeye salmon at the spawning grounds. Rainbow trout, which had been exercised, yielded greater value for β-hydroxybutyrate, and it was shown that under these conditions lactic acid interfered with the determination of β-hydroxybutyrate. Starvation of rainbow trout did not affect the concentration of β-hydroxybutyrate to any appreciable extent. In spawning salmon β-hydroxybutyrate showed some increase, as compared with fish in the pre-spawning stage of migration.

INTRODUCTION

Biochemical studies of the blood concentrations of sugar, protein, non-protein nitrogen, amino acid nitrogen (Jonas and McLeod, 1960), cholesterol, steroid hormones, and electrolytes (Idler and Tsuyuki, 1958) have been made in sockeye salmon during their spawning migration, but the concentration of ketone bodies, acetoacetate (AA) and β-hydroxybutyrate (HB), in salmon and other anadromous salmonoids has not been investigated. These fish undergo long periods of starvation during their spawning migration because, in general, they do not feed after they leave the sea. During this time, there is an increased mobilization of fats from the depots and decreased utilization of carbohydrates: conditions which favour ketogenesis (Chernick, 1961; Wakil and Bressler, 1962). It would therefore be interesting to know the ketone body concentrations in the blood of these fish during spawning migration. There appears to be no published information on the effect of starvation upon the concentration of ketone bodies in fish blood.

In the present study the concentration of ketone bodies was determined in the blood of sockeye salmon in the pre-spawning stage of migration and in fish on the spawning grounds. The effect of starvation upon the concentration of ketone bodies in the blood of rainbow trout was also examined.

METHODS AND MATERIALS

Fish

Two-year-old rainbow trout (*Salmo gairdnerii*) weighing 150–250 g were obtained from a commercial hatchery, where they had been fed the New

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Age complete trout fingerling pellets, distributed by J. R. Clark Co., Salt Lake City, Utah. The starvation experiments were started on December 15 and rainbow trout were held without feeding in a freshwater aquarium at 4–9 C. Sockeye salmon (*Oncorhynchus nerka*) were obtained at two different stages of maturation. Pre-spawning migrating fish were captured in the month of July at Robertson's Creek, Vancouver Island, B.C., as they arrived at Great Central Lake, and were kept in the freshwater aquarium at the laboratory for 2–4 weeks prior to killing. Spawning fish were obtained by skin divers at Great Central Lake, Vancouver Island, B.C., during October in 2 successive years. Blood was collected immediately after catching the fish. The number of fish employed in each experiment is indicated in the Tables and Figures.

Blood Collection

Of the rainbow trout and sockeye salmon held in the laboratory aquaria, blood was collected from fish which had been subjected to a minimum of exercise. The fish were caught with a net and immediately hit on the head to minimize struggling. The fish were bled by severing the caudal artery, care being taken to exclude slime. The blood of sockeye salmon caught by skin divers could not be obtained under the same controlled conditions, but the fish were bled as quickly as possible. In experiments reported in Table I,

Table I. Effect of exercise on the concentration of ketone bodies in the blood of rainbow trout.

	Fish No.	Acetoacetate and free acetone	β-hydroxy-butyrate
		Expressed as acetone (mg/100 ml)	
Not exercised	1	0.58	0.88
	2	0.54	1.26
	3	0.38	0.73
	4	0.41	0.97
	5	0.61	0.68
	6	0.46	–
		0.50 (0.08)[a]	0.90 (0.21)[a]
Exercised for 5 min and struggled in air for 5 min	7	0.74	2.28
	8	0.78	2.98
	9	0.28	2.00
	10	0.37	2.61
		0.54 (0.22)[a]	2.47 (0.37)[a]

[a]Mean value and standard deviation.

exercise was carried out by chasing the fish continuously for 5 min in a circular tank.

Determination of Ketone Bodies

Deproteinization of blood was carried out by the method of Somogyi (1945). Free acetone with AA and HB was determined by the method of Mayes and Robson (1957). The carbon tetrachloride (spectro grade) used was stored in a refrigerator to prevent deterioration. All glassware was thoroughly cleaned with chromic acid. Distilled water, freshly boiled and cooled, was used throughout the procedure.

The concentrations of ketone bodies are expressed in the conventional manner as milligrams of acetone per 100 ml blood. Acetone obtained by conversion of AA is determined together with preformed acetone present in the blood sample. The free acetone present in blood is known to be a product of spontaneous decarboxylation of AA in tissue extracts, rather than a true metabolite (Reid, 1962). The data for HB represent acetone formed by the conversion of this compound. The interference of lactic acid in the determination of HB is dealt with under Results and under Discussion.

RESULTS

In the preliminary stages of the investigation it was found that in a group of trout maintained under the same conditions, some fish had considerably higher concentrations of HB in the blood than others. This difference was subsequently found to be related to the degree of exercise of the fish prior to the collection of blood. The results (Table I) show that fish which had been severely exercised yielded much greater value for HB than fish which had not been exercised. However, even severe exercise did not have any effect on the concentration of AA. When lactic acid solution was substituted for blood, it did not result in the formation of any interfering material in the fraction corresponding to AA, but it did interfere in the determination of HB. A substance is formed from lactic acid reacting with 2,4-dinitrophenylhydrazine, which can interfere with the colorimetric determination of HB as acetone (Fig. 1). This interference, expressed as acetone, amounts to approximately 20 μg/mg of lactic acid.

Experiments conducted on the effect of starvation on the concentration of ketone bodies in the blood of rainbow trout are reported in Fig. 2 and 3. The first few days of fasting do not appear to produce any increase in the concentration of AA. It was noticeable that there was a tendency toward higher amounts of AA between the first and twelfth week of starvation. When the duration of starvation was extended for longer periods, there was, generally, greater variation between individual fish. The present experiments indicate that the concentration of AA in the blood of rainbow trout was between 0.3 and 1.0 mg/100 ml of blood and long periods of starvation do not appear to affect this level to any appreciable extent. The concentration of HB in trout

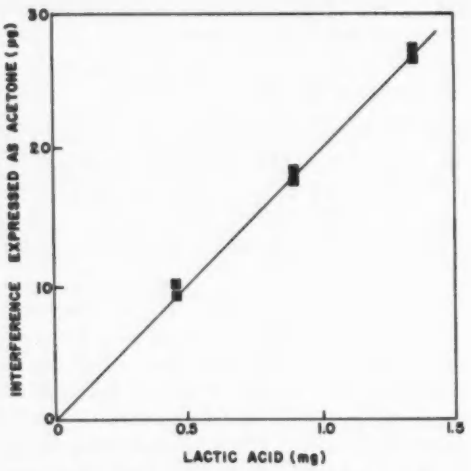

FIG. 1. Interference of lactic acid in the determination of β-hydroxybutyrate.

blood was higher than that of AA. It did not change when trout were maintained without food for 2 weeks and showed some decrease during long periods of starvation.

The results of the determination of ketone bodies in the blood of sockeye salmon are presented in Table II. They show well-marked differences between fish in the pre-spawning stage of migration and fish on the spawning grounds. In pre-spawning sockeye salmon, the AA concentration had an average value of 0.5 mg/100 ml of blood — within the range found for rainbow trout. Higher concentrations of AA, amounting to approximately 1.5 mg/100 ml of blood, were found in fish at the spawning grounds. In the pre-spawning sockeye salmon the concentration of HB amounted to 1.0 mg/100 ml blood and was higher than that of AA. In spawning salmon HB showed some increase, reaching approximately the same concentration as AA in fish under the same conditions. Differences due to sex and weight did not show any effect on the ketone body concentration in the trout and salmon used in these experiments.

DISCUSSION

The quantitative estimation of ketone bodies requires the conversion of the four-carbon acids to acetone, but none of the published methods appears to be completely satisfactory in this respect (Lehninger, 1957; Hird and Symons, 1959; Chernick, 1961). The conversion of HB to acetone by dichromate, employed in the present work, is a reaction which is not specific for HB. The higher values obtained for HB in exercised fish suggested the possible interference of lactic acid and it was shown that lactic acid could interfere in the determination of HB but not of AA. The concentration of lactic acid in fish

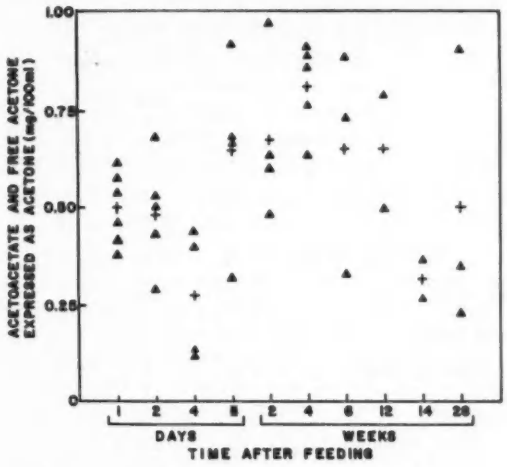

FIG. 2. Acetoacetate and free acetone in the blood of rainbow trout during starvation. Each point represents one fish; + = mean value.

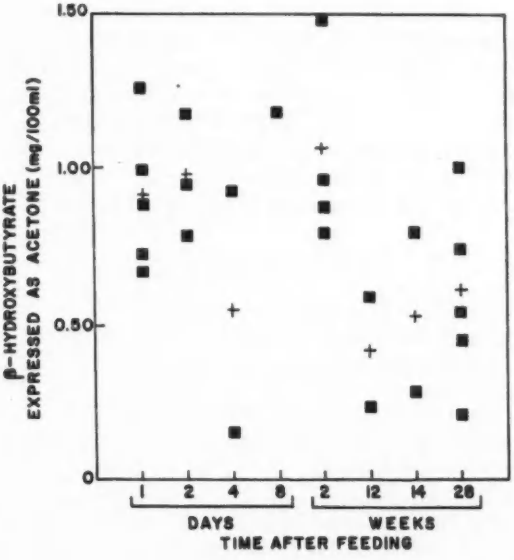

FIG. 3. β-hydroxybutyrate in the blood of rainbow trout during starvation. Each point represents one fish; + = mean value.

TABLE II. Ketone bodies in the blood of sockeye salmon.

Location and description	Fish No.	Acetoacetate and free acetone	β-hydroxy-butyrate
		Expressed as acetone (mg/100 ml)	
	1	0.30	0.65
	2	0.36	1.37
Obtained from Robertson's	3	0.51	1.53
Creek in 1964 and kept in	4	0.30	0.57
the laboratory aquarium	5	0.73	–
for 2–4 weeks	6	0.32	0.66
	7	0.67	1.14
	8	0.46	1.05
		0.46 (0.16)[a]	1.00 (0.35)[a]
	9	1.56	1.61
	10	1.82	1.87
Obtained from Great Central	11	1.57	1.13
Lake spawning bed in 1964	12	1.69	1.28
		1.66 (0.11)[a]	1.47 (0.28)[a]
	13	1.46	1.22
	14	1.30	1.86
Obtained from Great Central	15	1.48	–
Lake spawning bed in 1963	16	1.32	1.14
	17	1.69	1.77
	18	1.56	1.66
		1.47 (0.13)[a]	1.53 (0.26)[a]

[a]Mean value and standard deviation.

blood is comparable to that found in mammals and varies with the degree of exercise (Jonas and Tomlinson, 1962; see also Black, 1957; Black *et al.*, 1959). Although an attempt was made to limit the interference from lactic acid by minimizing the exercising of fish prior to collecting blood, the determinations of HB do not have the degree of accuracy obtained with AA. For this reason

the values for HB should be taken as indicative of approximate concentration only, but pronounced changes in concentration of HB would be reflected.

The concentrations of ketone bodies found in fish blood in the present work are the same as have been found in man and other mammals (Greenberg and Lester, 1944; Rosenthal, 1949). A recent report by Golovats'kii *et al.* (1963) also indicated that the ketone body concentration in carp and sazan is about the same as in warm-blooded animals. It is known that in man and some other mammals fasting or starvation are associated with a multifold increase in blood ketone bodies. The degree of change in ketone bodies varies considerably in different species of mammals, and it was suggested that ketone bodies may play a more or less prominent role in the starvation metabolism in these species (Fritz, 1961). Gammeltoft (1949) found a higher increase in blood ketones in starved human subjects and dogs than in other species examined. Rosenthal (1949) found a large increase in blood AA in the fasting rat and mouse, but the guinea pig showed much less response to fasting. There appears to be very little information on the effect of starvation on the concentration of ketone bodies in animals other than mammals. The present study with rainbow trout has shown that, in fish, starvation is not associated with any pronounced changes in ketone bodies. It has been known for some time that trout can resist long periods of starvation (Atkins, 1906; Titcomb *et al.*, 1928; Phillips *et al.*, 1953, 1959), but little is known about the accompanying biochemical changes. Phillips *et al.* (1959) have shown that the depletion of fat during starvation of trout is associated with an increase of the water content of the body. The higher concentration of AA and HB in the blood of sockeye salmon on the spawning grounds cannot be attributed solely to starvation, as a similar increase in concentration did not occur in rainbow trout subjected to a comparable period of starvation. The changes might be related to the specific physiological condition of spawning fish. It is known that an increase in ketone bodies could be due to hormonal disorders, but the changes observed in the present work are not as acute as in diabetes (Wakil and Bressler, 1962).

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Some Resemblances and Differences Between *Raja erinacea* and *Raja ocellata*, Including a Method of Separating Mature and Large-Immature Individuals of These Two Species[1]

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ABSTRACT

Raja erinacea Mitchill and *Raja ocellata* Mitchill are now distinguished by differences in tooth count and, in larger specimens, by size, size at sexual maturity, and eye spots when present in *R. ocellata*. The presence of distinct eye spots in the typical *R. ocellata* position in some *R. erinacea* was recorded. Separation of mature and large-immature male and female individuals of these two species was achieved by means of ventral pelvic denticles located in different positions in the two species, closer to the cloaca in female *R. erinacea* and more laterally on the pelvic fins in female *R. ocellata*. These pelvic denticles occur also in mature and maturing male *R. ocellata* but not in male *R. erinacea*. The denticles are much smaller and more numerous in *R. erinacea* and have relatively smaller sharp-angled bases with usually 4 and occasionally 5–6 rays. In *R. ocellata* the bases of the denticles are usually much larger, have 4–11 or more rays, usually with rounded tips.

INTRODUCTION

Raja erinacea Mitchill and *Raja ocellata* Mitchill are two closely related skates in which the only relatively sure means of specific identification at present, especially for small specimens, is by counting the number of rows of teeth. *Raja erinacea* has 38–64 rows in both upper and lower jaws, never more than 66 and usually less than 54 whereas *R. ocellata* has 72–110 rows (Bigelow and Schroeder, 1953).

Even this method of separation has been confused by the observation in Richards *et al.* (1963). In southern New England these authors used the number of tooth rows as in Bigelow and Schroeder (1953) to separate *erinacea* and *ocellata*. Upper jaw counts of *erinacea* from Block Island Sound were 47–64 and averaged 54 and those from Long Island Sound were 43–64 and averaged 52. However, they state that four skates received from the Miramichi Estuary of the Gulf of St. Lawrence, in which tooth counts (tooth-row counts on upper/lower jaw) were 72–76/69–76, resembled *R. erinacea* in most characteristics and that, with more data, a cline in tooth count may be demonstrated from the Miramichi region to Delaware Bay. For the latter region Fitz and Daiber (1963) had *erinacea* tooth counts of 42–61/40–51 with a mean of 50/46 for males and 50/48 for females. Other research workers have been in doubt about the separation of *erinacea* and *ocellata*. McKenzie (1959) said that in the outer Miramichi Estuary *Raja erinacea* is common, growing to a length of about 2 ft and occasionally longer. Most of the characteristics are

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those of *erinacea* but there are enough differences from the form of this species in more southern localities that these Miramichi skates might be considered a local race or even a subspecies of *erinacea*. He says that Mr William C. Schroeder has seen specimens and reports that the teeth and alar spine area of the Miramichi Estuary individuals resemble *ocellata*.

In 13 individuals from the Canadian area, which on the basis of *erinacea-ocellata* appearance and *erinacea*-type tooth count we have designated as *erinacea*, the range in tooth count was 44–55/47–54 and the average 50/50.

In 92 individuals of *ocellata* from the Canadian area separated from *erinacea* by the tooth count, and in many cases also by larger size or by immaturity at a large size, the tooth-count range was 68–95/68–104. Bigelow and Schroeder (1953) for their material of 32 specimens from the Massachusetts coast and Georges Bank noted that the usual number of rows of teeth in *ocellata* is 90–100, but in our material, consisting of 92 individuals from the Nova Scotian Shelf and Newfoundland, 89% of the tooth counts were below 87, and 82% between 72 and 86.

There is thus a useful range of separation in tooth count between the two species which, however, might be narrowed by examination of larger numbers.

Other characteristics which have been used to assist in the separation of *erinacea* from *ocellata* often cannot be used with certainty to distinguish between individuals. The usual length at sexual maturity of both sexes of *erinacea* is 450–500 mm and the largest individuals of *erinacea*, especially in the southern part of its habitat, are well below 600 mm. *Ocellata*, on the other hand is reported not to mature before a length of 620–660 mm is reached. The greatest recorded length of *ocellata* is 1090 mm (Bigelow and Schroeder, 1953). Richards *et al.* (1963) noted that, in southern New England, at 40–54 cm *erinacea* is mature and *ocellata* is immature.

Our largest specimen of *erinacea*, from the Nova Scotian Shelf, was 574 mm long and our largest individual of *ocellata*, from Hermitage Bay on the south coast of Newfoundland, was a male 1129 mm long. Although our numbers and range of sizes were too few for a detailed statement, the generally smaller size of *erinacea* at sexual maturity is evident in our data. In the *ocellata* that we have examined from the Canadian area sexual maturity is unusual before a length of 70 cm.

Raja ocellata received its specific name from the presence of ocelli or eye spots on the dorsal surface, typically a pair on the posterior parts of the pectorals, but sometimes there are other eye spots on the pectorals, pelvics, or elsewhere. These eye spots are whitened areas, sometimes with a black dot at the centre, and usually surrounded by a group of dark spots which may run together to form a ring. It has hitherto been assumed that skates of the *ocellata-erinacea* group with such eye spots on the pectorals are *R. ocellata*. Bigelow and Schroeder (1953) said that these ocellar spots, usually present on the upper surface of the disc are a reliable means of identification for specimens that have them but that specimens lacking these spots resemble *erina-*

cea so closely that they must be distinguished by the number of teeth. Because, as we shall demonstrate, eye spots may be present also in *erinacea*, some field determinations of small- to medium-sized *ocellata* by means of the general resemblance to *ocellata-erinacea* and the presence of eye spots have probably been in error.

EYE SPOTS AND COLOUR OF UPPER SURFACE

Raja ocellata. The upper surface in the few individuals of *ocellata* for which the background colour was noted varies as in *erinacea* from light brown to brownish grey. *Erinacea* may be more deeply coloured but we have not seen enough fresh specimens of both species at the same time to be certain of the general application of this observation. Also, the colour presumably varies with depth of capture. The observation agrees, however, with the descriptions of Bigelow and Schroeder (1953) for the background colour in *ocellata* as light brown above, and for the upper surface of *erinacea* as greyish to dark brown or clouded with light and dark brown.

The size and arrangement of the interspersed black dots (Fig. 1–6) vary in the manner that will be described in detail for *erinacea*. Some of the largest individuals of *ocellata* are so much larger than the largest *erinacea* that *ocellata*, on the average, has a greater number of black dots at the largest sizes but individuals of both species vary widely in the numbers of black dots present.

In our earlier investigations, presence or absence of eye spots on the dorsal surface was recorded for only 64 of 112 *ocellata* from the Canadian area and it cannot be assumed that the recording of the presence or absence of eye spots was entirely at random. Of 64 specimens examined 61% possessed eye spots. However, in 34 specimens examined later (32 from the Canadian area and two from Georges Bank), for which the presence or absence of eye spots was observed for all individuals, eye spots were present in 53%. Thus, the error due to lack of complete records of presence or absence of eye spots in the first group of observations was probably not great. The two groups are combined for the relation of eye spots to size and sex in Table I.

The five individuals in the 21–40-cm group, all without eye spots, were obtained in the one inshore area at Bristol's Hope Cove, Conception Bay, Newfoundland. It is possible at the smallest sizes, with few dark spots, that these spots are often too few to be arranged in eye-spot rings. In sizes over 40 cm, in the small number of fish examined, there is little reason in these data to suspect that a change occurs in the possession of eye spots with increase in size or that the possession of eye spots is affected by sex or sexual maturity. There is a small increase with size and sexual maturity in the percentage of females with eye spots but in the absence of such an increase in males more data are needed.

There was a distinct tendency for the eye spots to occur in pairs, usually 1 pair (40%) or 2 pairs (11%), but 3 had 3 pairs, 1 possessed 4 pairs, and 1 had 11 and another 13 eye spots (Table II). The paired eye spots are typically on the posterior parts of the pectorals in the position shown in Fig. 1–4. Even

TABLE I. Numbers of male and female *Raja ocellata* of various sizes with and without eye spots on the dorsal surface.

Length range	Total *ocellata*			Eye spots present	Eye spots present male	Eye spots present female	Mature
	Male	Female	Total				
cm	*no.*	*no.*	*no.*	%	%	%	%
21–40	1	4	5	0	0	0	0
41–60	11	6	17	59	64	50	0
61–80	11	24	35	69	91 } 63	58	29
81–110	19	22	41	56	47 }	64	98
Total omitting 21–40 cm	41	52	93	61	63	60	

where larger numbers of white spots occur, which have been included as eye spots in Table II, the pair of eye spots on the posterior parts of the pectorals is as a rule present and usually the largest and most typical of the group (Fig. 2, 5, 6). The presence of additional eye spots in *ocellata* is also noted by Bigelow and Schroeder (1953).

In 14 out of 17 cases in which 4 or more eye spots were present there was a pair of eye spots on the pelvic fins as well as the usual pair on the posterior pectorals, and in the one specimen possessing 3 eye spots the unpaired spot was on the pelvic. In 7 out of these 17 specimens an additional pair of eye spots, smaller than the usual pair, occurred anterior to the axils of the pectorals (Fig. 2, 6), and in 2 of the remaining 10 specimens there was 1 eye spot in this position.

The typical pair of eye spots, situated posteriorly on the pectorals, may have predominantly white central areas (Fig. 1–3, 5–6), in some cases with a black dot at the centre (Fig. 3, 5), greyish white centres or very occasionally centres of approximately the same greyish colour as the dorsal surface (Fig. 4). Generally, but not always, dark pigment spots similar to those of the dorsal surface are arranged around the rim of the whitish central area to form a typical eye spot. If the black spots run together a ring is formed (Fig. 2, 3 left, 4 and 6), but sometimes as in Fig. 1 there are only white eye spots on the darker surface with no alteration in the pattern of dark pigment spots. All gradations between these two extremes occur.

Raja erinacea. The general background colour of the dorsal surface in our specimens ranged from light brown to brown and from brownish-grey to greyish-brown.

On this general background are dark spots ranging from few as in Fig. 9 (few and indistinct in our smallest individual — Templeman, 1965) to intermediate numbers of distinct dots as in Fig. 7 and 8 and to large numbers

TABLE II. Frequency of eye spot numbers in male and female *Raja ocellata* 41 cm and over (omitting the five specimens, one male and four females, 21–40 cm long none of which had eye spots).

Eye spots	Males	Females	Total	Males	Females	Total
no.	*no.*	*no.*	*no.*	%	%	%
0	15	21	36	37	40	39
1	0	2	2	0	4	2
2	18	19	37	44	37	40
3	0	1	1	0	2	1
4	6	4	10	15	8	11
5	0	1	1	0	2	1
6	1	2	3	2	4	3
8	0	1	1	0	2	1
11	1	0	1	2	0	1
13	0	1	1	0	2	1
Total:	41	52	93	100	101	100

as in Fig. 10. Often on large individuals there is a fairly straight row of dots down the mid-dorsal line in the region occupied by the mid-dorsal spines of the smaller *erinacea* (Fig. 8, 10).

In a group of nine *erinacea* and two *ocellata* from Browns Bank it was noted that the black dots on the *erinacea* were sharper and much more distinct than those on *ocellata*. At present we cannot be certain of the general application of this observation. Many of the black dots in both *erinacea* and *ocellata* apparently originate around the bases of spines which may later fail to grow in size and may disappear. In our figures this is seen best in Fig. 7 which shows an *erinacea* of intermediate size in which both spots and spines are well developed.

The size of the dark dots may vary from tiny spots about 1 mm in diameter to spots about 8 mm or occasionally greater in diameter. The most common sizes are between 2 and 6 mm in diameter. The range of black spot sizes and numbers on the dorsal surface of *erinacea* includes approximately the whole range or overlaps greatly the range of black spot numbers and sizes found in *ocellata*; and hence the number, size, and distribution of these dots offer no means of separating the two species.

Although eye spots are mentioned in the literature as characteristic of *ocellata* rather than *erinacea*, of our 12 individuals of *erinacea* from the Nova Scotian Shelf, three possessed a pair of eye spots in the typical position of

ocellata on the posterior parts of the pectorals (Fig. 9, 10 and Table III). All three were definitely *erinacea*, sexually mature at sizes smaller than those for *ocellata*, and with tooth counts much lower than those of *ocellata* (54-cm female, tooth count 52/52; 56-cm male, tooth count 47/47; and 57-cm male, tooth count 55/54). In 85 *erinacea* from Georges Bank, however, only three possessed a pair of eye spots on the posterior parts of the pectorals. The eye spots of the Nova Scotian Shelf *erinacea* were as distinct as those in *ocellata* but the eye spots of the three specimens of *erinacea* from Georges Bank were faintly marked and indistinct. In all cases the eye spots were in the normal *ocellata* position on the posterior parts of the pectorals, and only one pair of eye spots was present. Mr William C. Schroeder (personal communication) said that he remembers trawling one or two *erinacea* with eye spots a few years ago in the offing of Nantucket.

PELVIC DENTICLES

Occurrence and Location

On April 24, 1963, while examining a group of nine *erinacea* and two *ocellata* from the Nova Scotian Shelf we noted a group of small spines or denticles (subsequently called pelvic denticles, denticles, or denticle patch) on the ventral surface in the cloacal–pelvic region of the larger females. Moreover,

Table III. Numbers of male and female *Raja erinacea* of various sizes with or without eye spots on the dorsal surface.

	Eye spots present				Eye spots absent			
Length range	Male	Female	Total	Total mature	Male	Female	Total	Total mature
cm								
	Nova Scotian Shelf 1962–63							
31–40	...	...	...	...	1	2	3	0
41–50	...	...	...	...	1	0	1	1
51–60	2	1	3	3	1	4	5	4
Total:	2	1	3	3	3	6	9	5
	Georges Bank 1964							
31–40	1	...	1	0	1	2	3	0
41–50	1	1	2	2	32	35	67	47
51–60	...	...	...	...	2	10	12	10
Total:	2	1	3	2	35	47	82	57

there were differences in the appearance and location of these denticles in the two species. Subsequent observations on *erinacea* and *ocellata* from other areas have confirmed these differences.

FEMALE *Raja erinacea*. In female *R. erinacea* these pelvic denticles first appear at the posterior bases of the pelvic fins, mainly to the anterior right (or left on the opposite side) of the posterior axils of the pelvic fins and obliquely posterior to the cloaca (Fig. 11, 12). In this early and immature stage, with the cloaca usually tiny, the denticle patch is a little closer to the cloaca than to the lateral edge of the pelvic fin but the distances are not greatly different. With increasing sexual maturity, denticles develop as far posterior as the axils of the pelvics (Fig. 12D, 13A) and later extend on the pelvic fins posterior to the axils of the pelvics (Fig. 13) and partly across the base of the tail posterior to the cloaca (Fig. 13C,D; 14A). Because at the same time that the denticle patch is growing the cloaca is enlarging, the mediad edge of the fully developed denticle patch comes close to the edge of the cloaca (Fig. 13B,C,D; 14A). The denticles now cover a large part of the smooth area between the cloaca and the medial part of the pelvic fin. The denticles extending over this smooth central area between the base of the pelvic fin and the cloaca are closely aligned in little individual pits and, at least laterally, in rows leading toward the postero-lateral borders of the pelvic fin. It is indicated also in Fig. 14 that these denticles tend to be in rows over the smoother pelvic surface near the cloaca.

At the same time that the denticle patch is approaching the cloaca it is extending laterally and posteriorly on to the base and surface of the pelvic fin (Fig. 13, 14). The first extensions of the denticle patch on to the pelvic fin run in the grooves between the rays of the pelvic fin. This is especially visible anteriorly. Later the denticle patch on the pelvic fin expands to cover also the flatter surface between the main grooves (Fig. 13, 14).

In female *erinacea* with a large cloacal opening and which presumably have been mature for some time, the denticle patch in its greatest degree of expansion extends on each side from immediately anterior to the posterior axil of the pelvic on to the base of the tail behind the cloaca. It closely borders the cloaca in a shallow curve extending somewhat in front of the cloaca and diagonally backward and laterally to cover the inner half of the base of the posterior half of the pelvic fin.

All 52 female *erinacea* (36–55 cm) examined possessed some evidence of these pelvic denticles (Table IV). The smaller immature females (36–45 cm) tended to have small or very small patches of pelvic denticles. Presumably still smaller sizes would have had no pelvic denticles. Some of the smallest mature females (including one with egg cases) also had small patches of pelvic denticles whereas most mature females at the largest sizes had very well-developed patches (Table IV).

The mature female *erinacea* from the Nova Scotian Shelf and from Georges Bank were approximately similar in the location of the patches of pelvic denticles, but only four of the 52 female *erinacea* of Table IV were from the

TABLE IV. Presence or absence of ventral pelvic denticles in *Raja erinacea* and *Raja ocellata*. (A, pelvic denticles absent; V, very small patch; S, small patch; I, patch of intermediate size; L, large adult-type patch of pelvic denticles. $\frac{L}{16}$ = 16 skates with large patch of pelvic denticles. The L, I, etc. used for male *ocellata* are relative only to the sizes of the ventral pelvic denticle patches in male *ocellata* which are much smaller than the fully developed patches in the mature females.)

Length range	Male			Female		
	Immature	Immature maturing	Mature	Immature	Immature-maturing	Mature
cm						
	R. erinacea					
16–20	$\frac{A}{1}$					
36–40	$\frac{A}{3}$			$\frac{V}{2}$ $\frac{S}{1}$		
41–45	$\frac{A}{4}$	$\frac{A}{1}$	$\frac{A}{6}$	$\frac{V}{2}$ $\frac{S}{2}$ $\frac{I}{1}$		$\frac{L}{1}$ $\frac{V^a}{1}$ $\frac{S}{1}$ $\frac{I}{2}$ $\frac{L}{1}$
46–50	$\frac{A}{2}$		$\frac{A}{21}$	$\frac{S}{1}$ $\frac{I}{2}$ $\frac{L}{2}$		$\frac{L}{2}$ $\frac{S}{1}$ $\frac{I}{1}$ $\frac{L}{16}$
51–55	$\frac{A}{1}$		$\frac{A}{2}$	$\frac{I}{1}$	$\frac{I}{1}$	$\frac{I}{2}$ $\frac{L}{9}$
56–60			$\frac{A}{2}$			
	R. ocellata					
21–30			$\frac{A}{1}$			
31–40	$\frac{A}{1}$		$\frac{A}{3}$			
41–50	$\frac{V^b}{1}$					
51–60				$\frac{S}{1}$		
61–70					$\frac{I}{1}$	
71–80			$\frac{I}{1}$ $\frac{L}{1}$	$\frac{I}{1}$ $\frac{L}{1}$	$\frac{V}{1}$	$\frac{L}{1}$ $\frac{V}{1}$ $\frac{S}{2}$ $\frac{L}{7}$
81–90			$\frac{A}{2}$ $\frac{L}{6}$			$\frac{L}{1}$ $\frac{S}{3}$ $\frac{I}{2}$ $\frac{L}{6}$
91–100		$\frac{A}{1}$	$\frac{L}{2}$			

[a]Complete egg cases present in oviducts.
[b]Two only, denticles on left, none on right.

FIG. 1–23

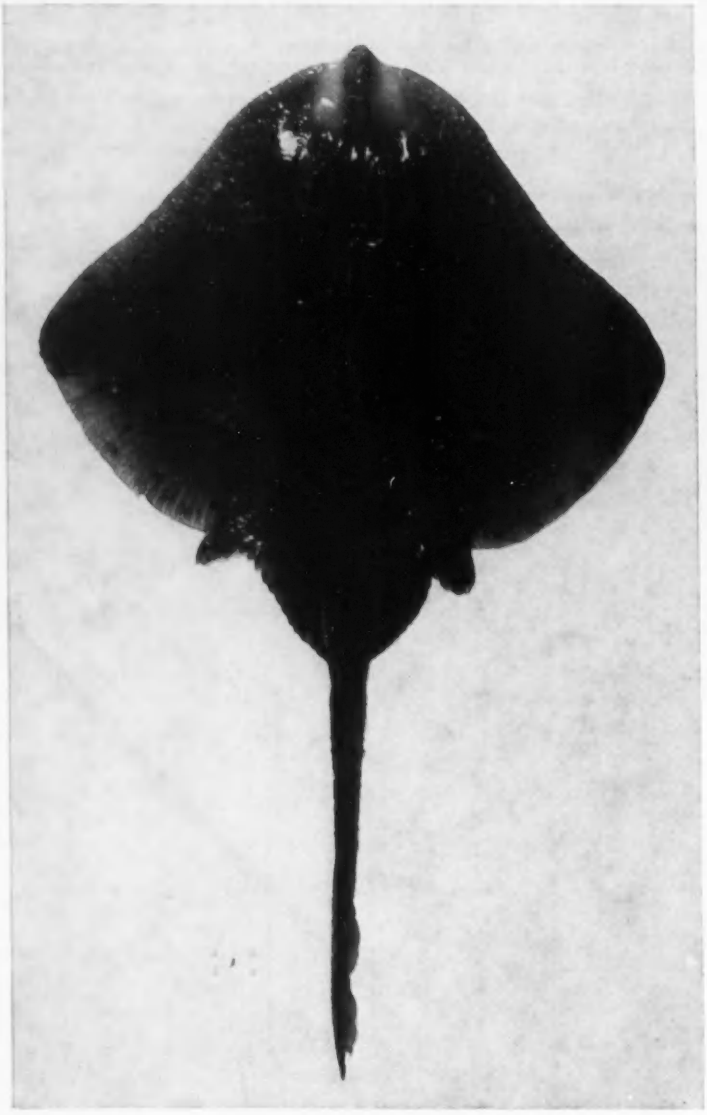

FIG. 1. *Raja ocellata* in dorsal view, showing paired eye spots in normal position, a small number of dorsal pigment spots, and a complete row of median dorsal spines. (Total length 44.1 cm, male immature, tooth count (number of rows of teeth on upper/lower jaw) 84/82, *A. T. Cameron*, Nova Scotian Shelf, 43°47′15″N, 59°57′00″W, 27–33 m, November 21, 1962.)

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FIG. 2. *Raja ocellata* in dorsal view, showing paired eye spots in usual position on pectorals, two smaller eye spots above the axils of the pectorals, one on the upper right of the pectoral and a small number of dorsal pigment spots. (Total length 53 cm, female immature, tooth count 77/, *Investigator II*, off Topsail Beach, Conception Bay, Nfld., 6–13 m, August 25, 1948.)

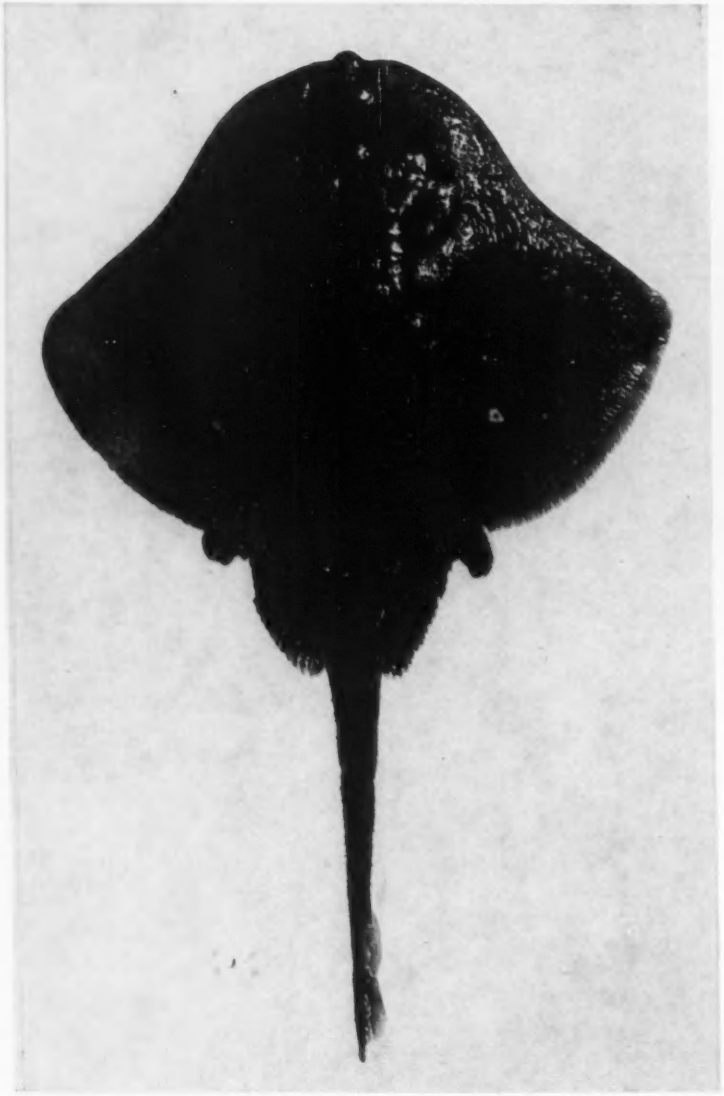

FIG. 3. *Raja ocellata* in dorsal view, showing paired eye spots in the normal position and a large number of dark pigment spots. (Total length 83.9 cm, female immature, tooth count 76/79, *A. T. Cameron*, Nova Scotian Shelf, 44°01′30″N, 61°37′30″W, 90 m, March 8–9, 1963.)

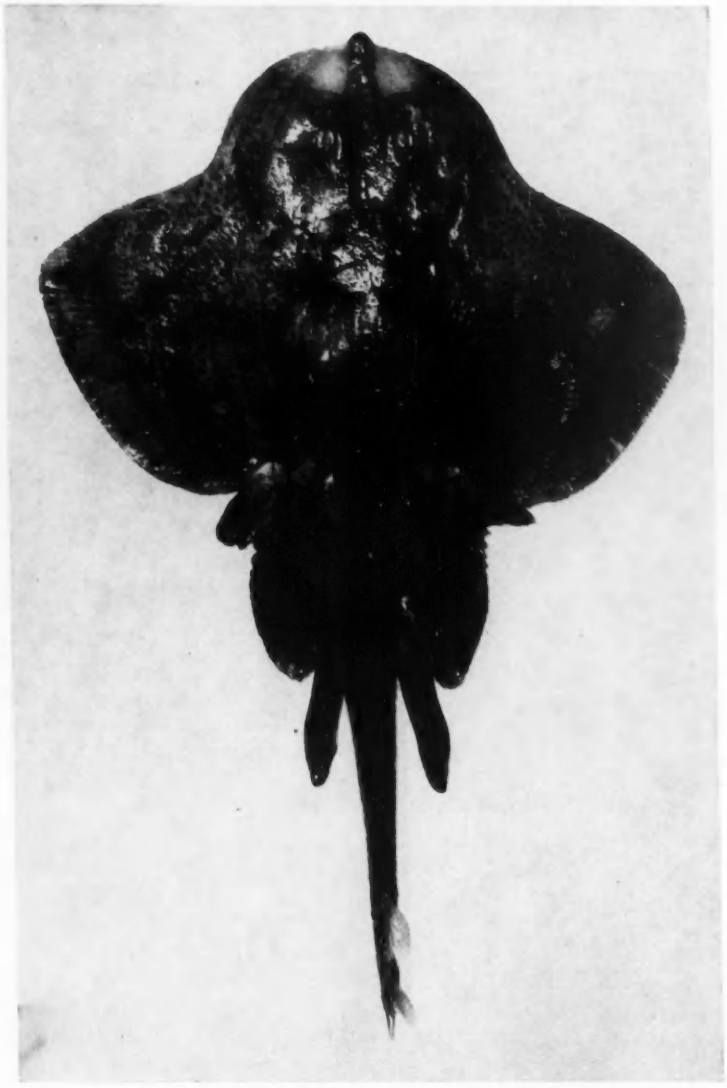

FIG. 4. *Raja ocellata* in dorsal view, showing one pair of eye spots in the normal position and a moderately large number of dark pigment spots. (Total length 100 cm, male mature, tooth count 73/73, *Investigator II*, Sable Island Bank, 44°02′30″N, 60°54′00″W, 46 m, May 12, 1950. The large black spot to the left of the left eye spot is an artifact.)

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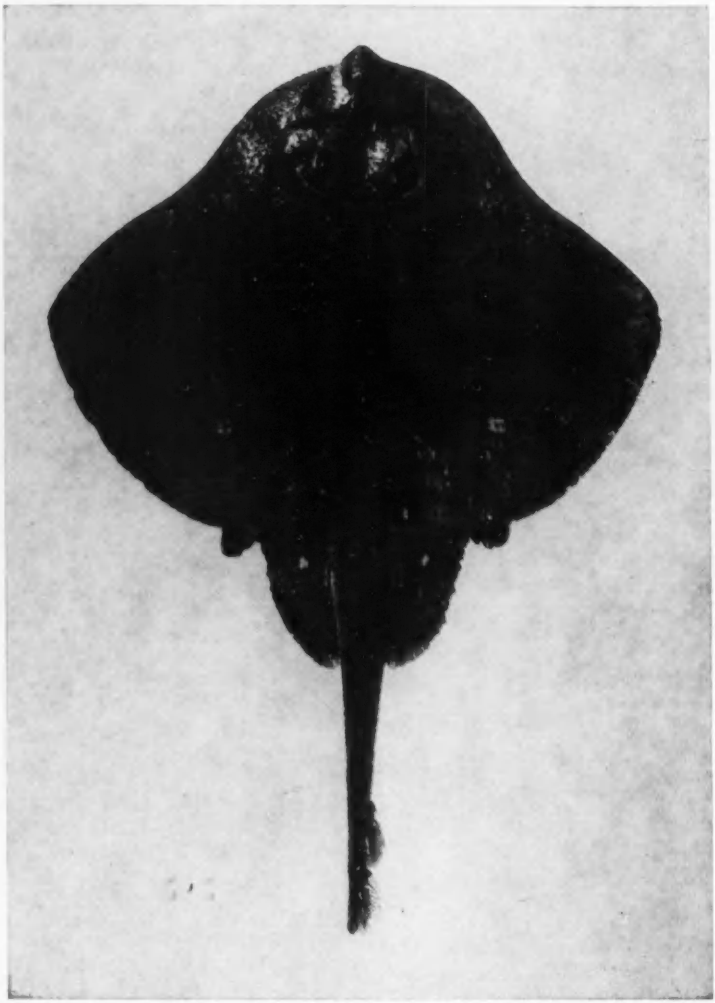

FIG. 5. *Raja ocellata* in dorsal view, with eye spots in the normal position on the pectorals and a distinct pair on the pelvics. (Total length 79.0 cm, female mature, tooth count 75/77, Twillingate, Notre Dame Bay, Nfld., 18–27 m, July 4, 1964.)

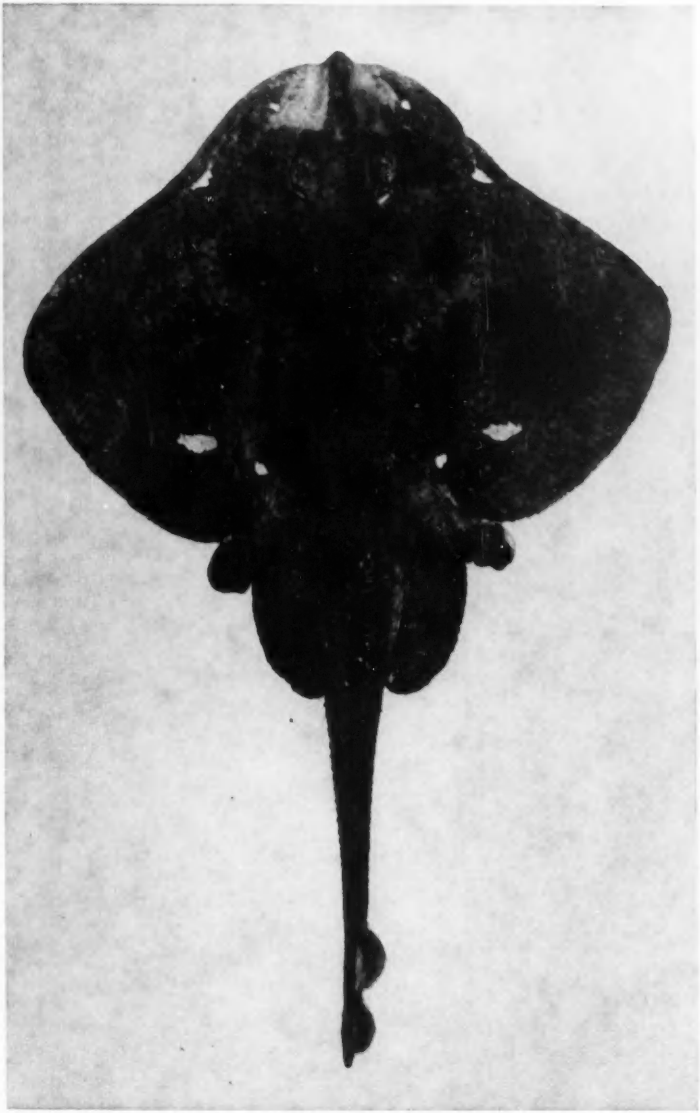

FIG. 6. *Raja ocellata* in dorsal view, with unusually large eye spots in the normal position on the pectorals, an additional smaller pair above the axils of the pectorals and two additional pairs anteriorly. (Total length 94 cm, female mature, tooth count 73/74, trawler *Blue Foam*, St. Pierre Bank, 45°05′N, 56°08′W, 187–214 m, February 13, 1953.)

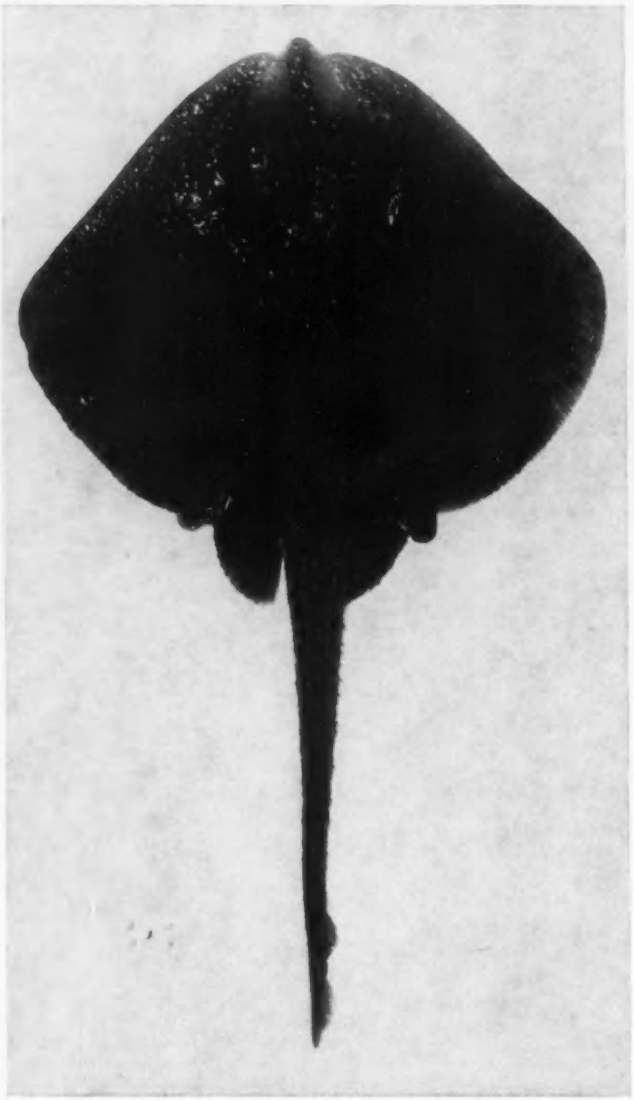

FIG. 7. *Raja erinacea* in dorsal view, without eye spots, showing the retention of the general spiny appearance of the disc and of the complete row of median dorsal spines. (Total length 37.3 cm, female immature, tooth count 48/47, *A. T. Cameron*, western portion Browns Bank, 53–119 m, March 1963.)

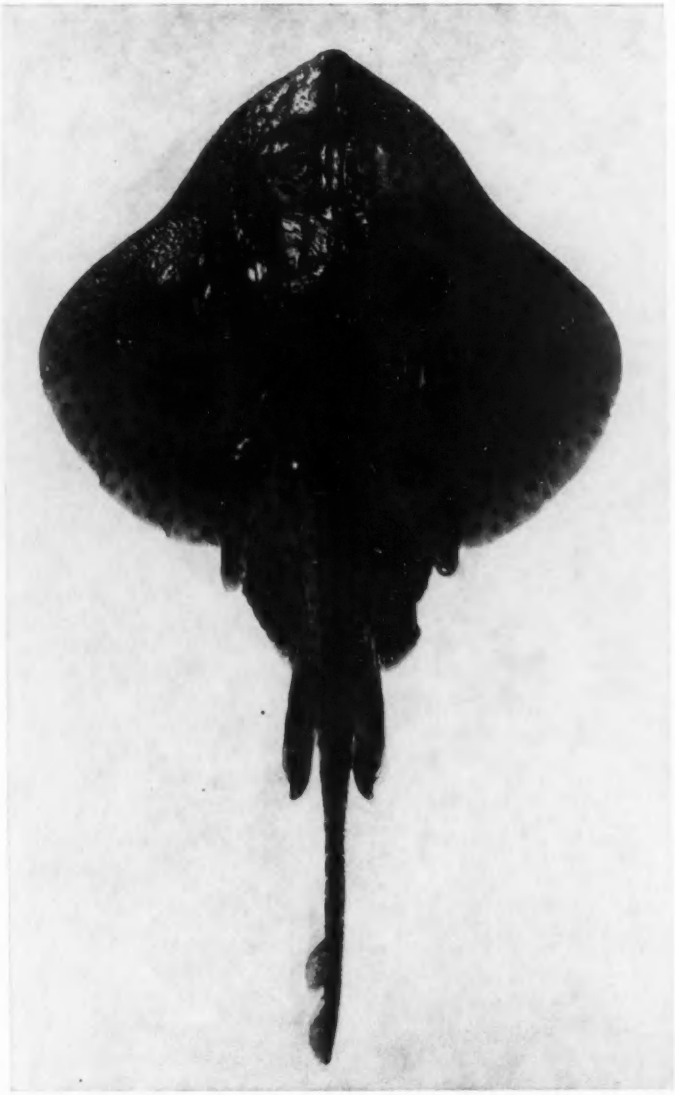

FIG. 8. *Raja erinacea* in dorsal view, without eye spots, showing young male adult appearance with the disc generally smooth except for localized groups of spines and with the median dorsal spines absent except for a few small spines anteriorly and posteriorly. (Total length 46.7 cm, male mature, tooth count 47/47, *A. T. Cameron*, western portion Browns Bank, 53–119 m, March 1963.)

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FIG. 9. *Raja erinacea* in dorsal view, with eye spots in the normal *ocellata* position on the pectorals. (Total length, 54.3 cm, female mature, tooth count 52/52, *A. T. Cameron*, Nova Scotian Shelf, 43°47′15″N, 59°57′00″W, 27–33 m, November 21, 1962.)

FIG. 10. *Raja erinacea* in dorsal view, with eye spots in the normal position on the pectorals. (Total length 57.4 cm, male mature, tooth count 55/54, *A. T. Cameron*, western portion Browns Bank, 53–119 m, March 1963.)

FIG. 11. *Raja erinacea* in ventral view × 2.0 showing early stage left pelvic denticle patch. (Total length 37.3 cm, female immature, weight of two shell glands 0.1 g, tooth count 48/47. *A. T. Cameron*, western portion Browns Bank, 53–119 m, March 1963.)

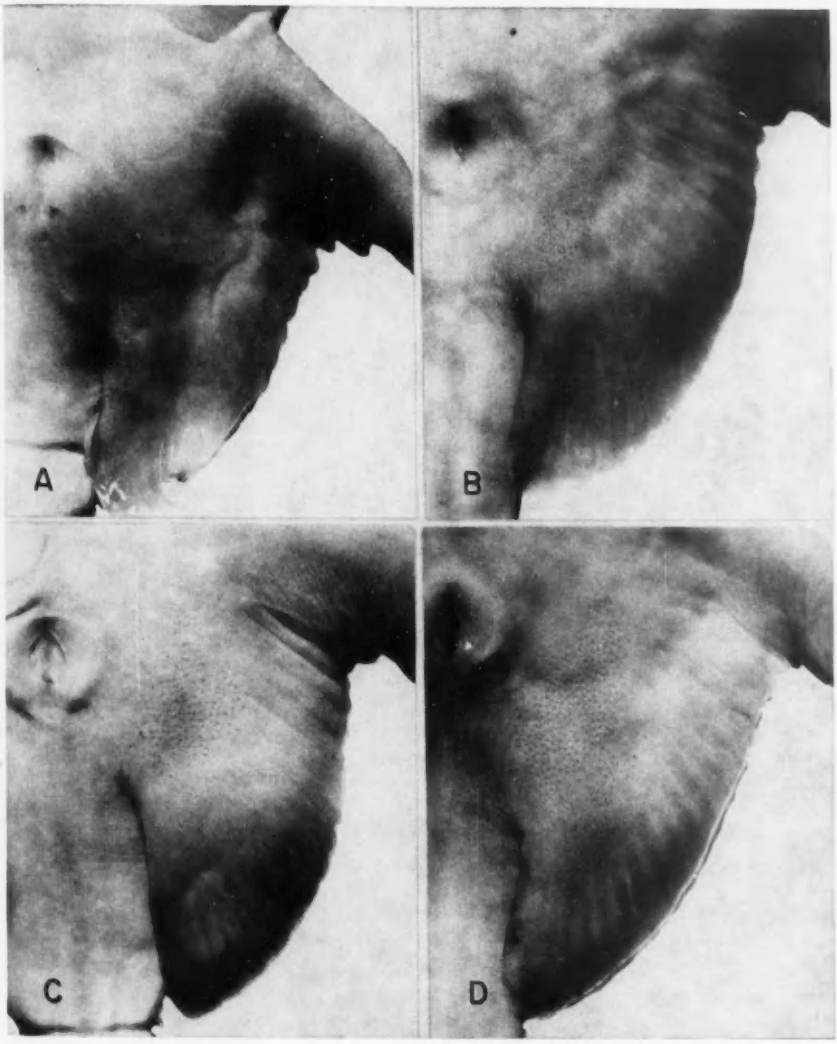

FIG. 12. *Raja erinacea* in ventral view, natural size, *A. T. Cameron*, eastern edge Georges Bank, 70–128 m, August 12–21, 1964, showing a series of increasing stages of the early development of the left patch of pelvic denticles, natural size:

	Total length	Sex and maturity	Diameter largest egg	Weight two shell glands	Tooth count	
					Upper	Lower
	cm		*cm*	g	*no.*	*no.*
A.	44.7	F immature	<0.1	<0.1	48	47
B.	42.3	F immature	0.1	<0.1	46	46
C.	46.3	F immature	0.15	1.0	52	48
D.	48.1	F immature	<0.1	<1.0	49	48

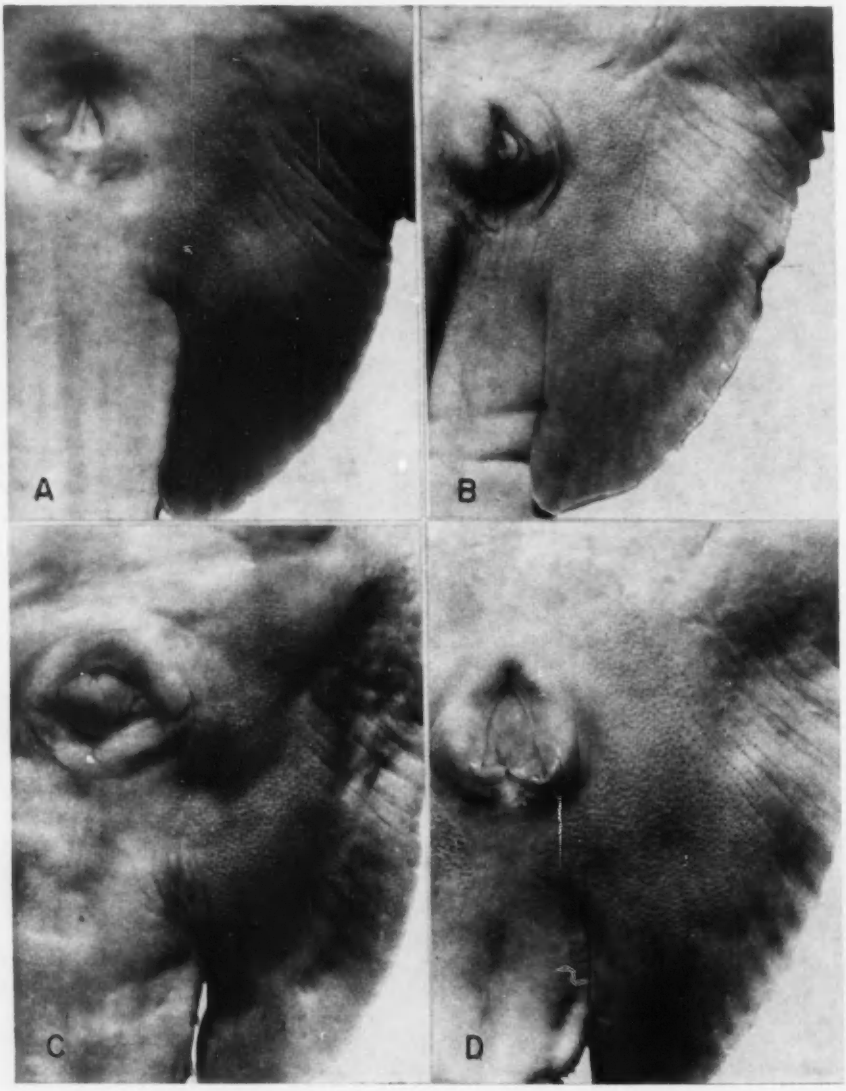

FIG. 13. *Raja erinacea* in ventral view, *A. T. Cameron*, eastern edge Georges Bank, 70–128 m, August 12–21, 1964, showing a series of increasing stages of development of the left patch of pelvic denticles, natural size:

	Total length	Sex and maturity	Diameter largest egg	Weight two shell glands	Tooth count	
					Upper	Lower
	cm		*cm*	*g*	*no.*	*no.*
A.	44.7	F mature	mature size (broken)	10	50	47
B.	47.5	F immature	0.8	4	52	48
C.	46.3	F mature	mature size (broken)	16	51	47
D.	48.5	F mature	mature size (broken)	16	51	48

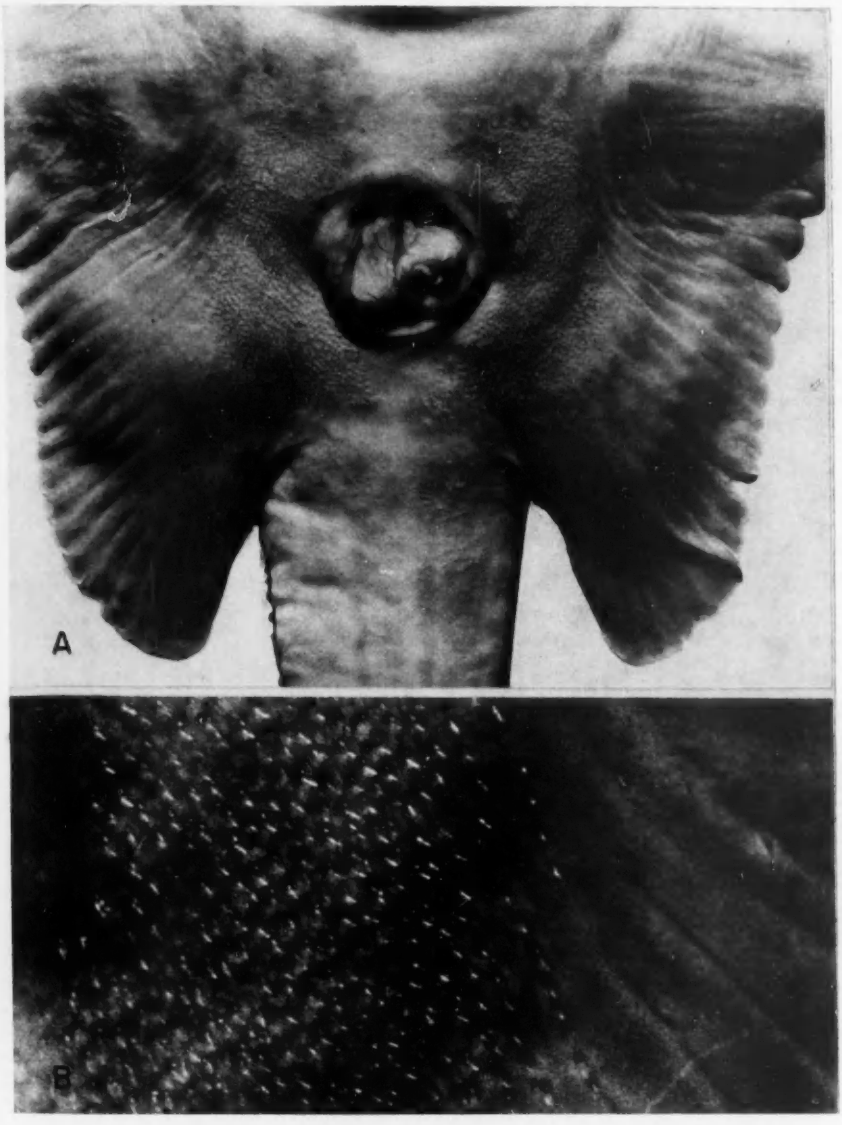

FIG. 14. *Raja erinacea* in ventral view, showing development of pelvic denticles in a mateur specimen. (A, natural size, complete pelvic denticle patches and B × 5.0, portion of the left patch of a mature female, total length 52.7 cm, tooth count 52/48, *A. T. Cameron*, western portion Browns Bank, 53–119 m, March 1963.)

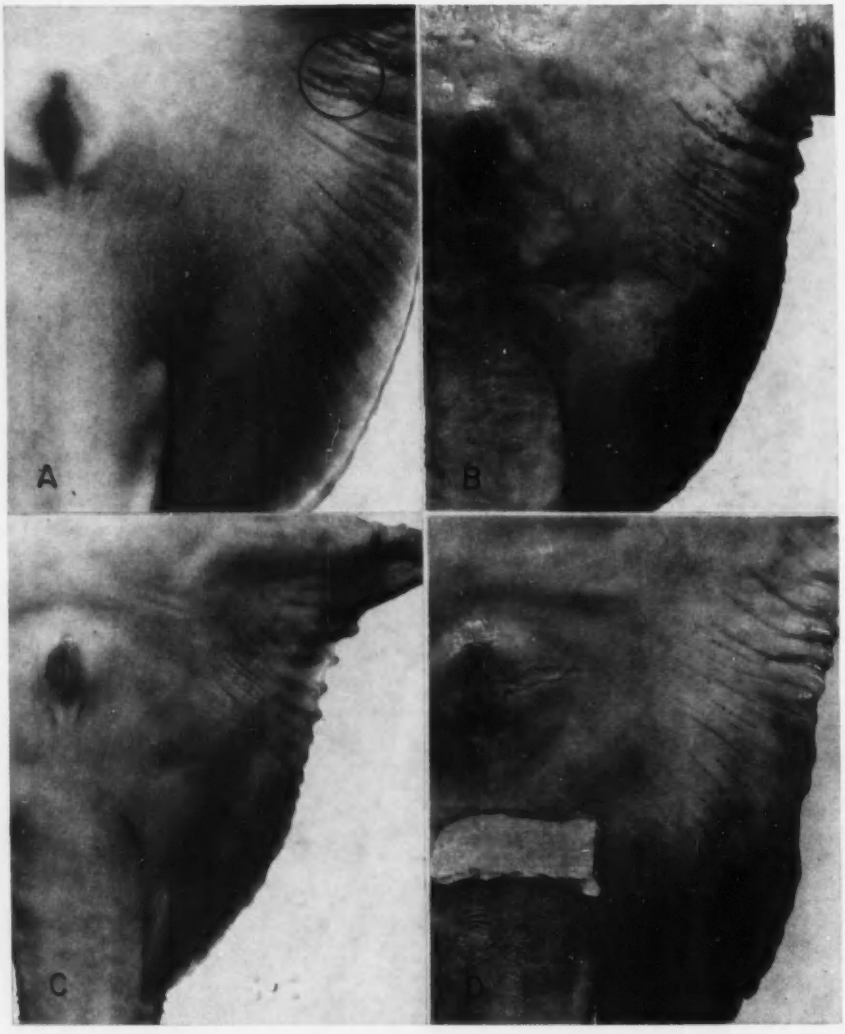

FIG. 15. *Raja ocellata* in ventral view, showing gradual development of the left patch of pelvic denticles. (A, natural size, and C × 0.5, *A. T. Cameron*, eastern edge of Georges Bank, 70–128 m, August 12–21, 1964; B and D × 0.5, *Investigator II*, Trepassey Bay, Nfld., 4–18 m, August 11–13, 1964.)

	Total length	Sex and maturity	Diameter largest egg	Weight two shell glands	Tooth count	
					Upper	Lower
	cm		*cm*	*g*	*no.*	*no.*
A.	55.8	F immature	<0.1	<0.01	80	79
B.	82.3	F mature	1.6	57	79	76
C.	71.5	F immature	0.4	1.0	77	78
D.	86.8	F mature	2.7	115	72	77

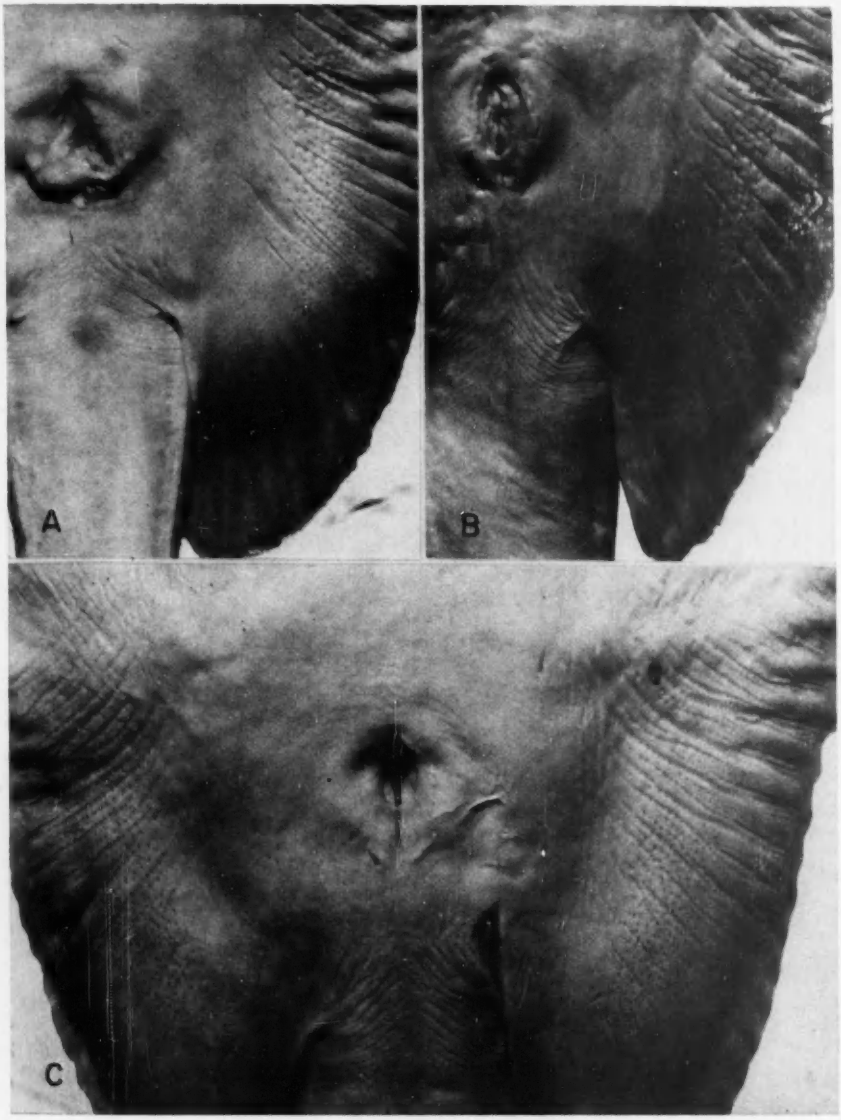

FIG. 16. *Raja ocellata* in ventral view × 0.6, showing greater development of the patches of pelvic denticles. (A, Twillingate, Notre Dame Bay, Nfld., 18–27 m, July 4, 1964; B, *A. T. Cameron*, Nova Scotian Shelf, 44°01′30″N, 61°37′30″W, 90 m, March 8–9, 1964; C, *Investigator II*, Trepassey Bay, Nfld., 4–18 m, August 11–13, 1964.)

	Total length	Sex and maturity	Diameter largest egg	Weight two shell glands	Tooth count	
					Upper	Lower
	cm		*cm*	*g*	*no.*	*no.*
A.	79.0	F mature	3.0	114	78	78
B.	83.9	F immature			76	79
C.	79.7	F mature	Broken but mature size	79	84	90

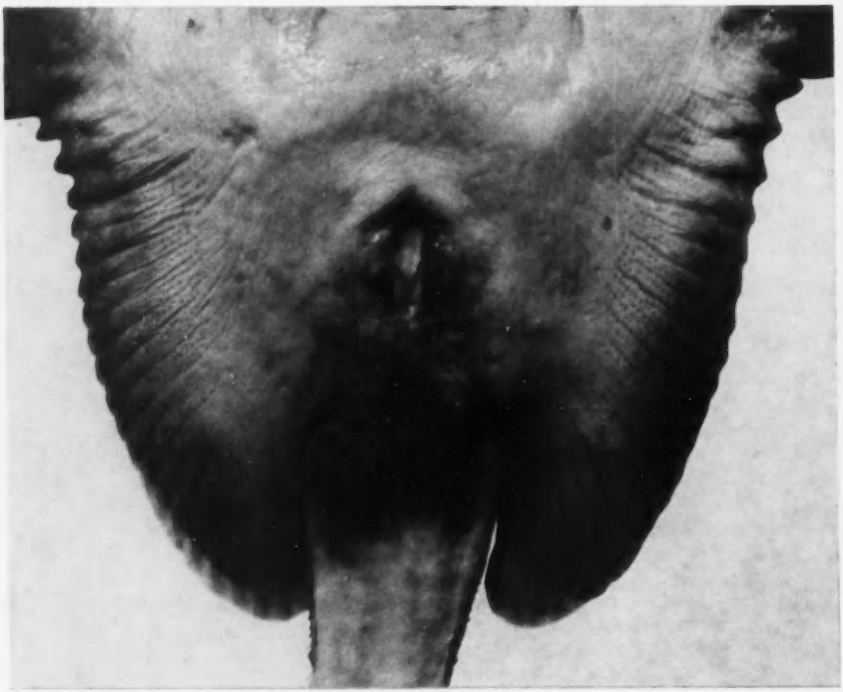

FIG. 17. *Raja ocellata* in ventral view × 0.5 showing development of pelvic denticles in a mature female. (Total length 78.6 cm, female mature, diameter largest egg 2.4 cm, weight of two shell glands 81 g, tooth count 81/85, *Investigator II*, Trepassey Bay, Nfld., 4–18 m, August 11–13, 1964.)

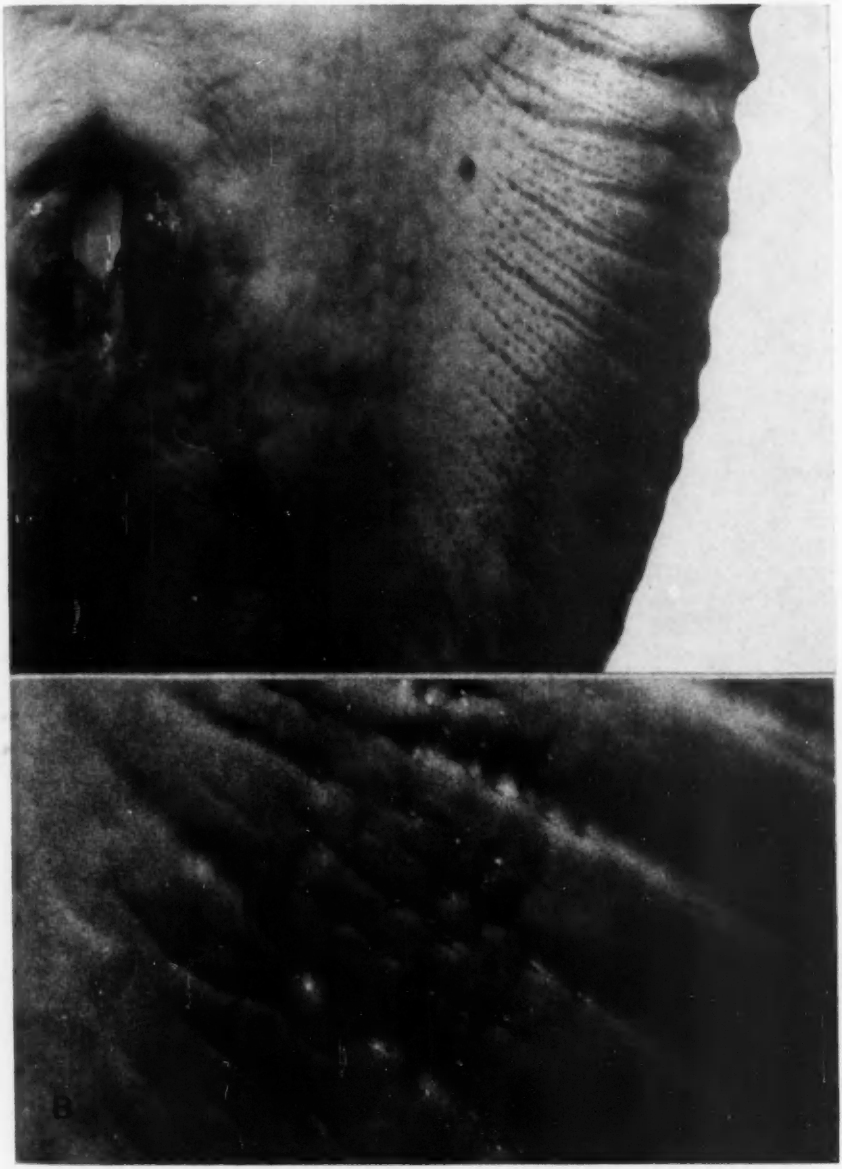

FIG. 18. *Raja ocellata* in ventral view, showing A × 0.9, the left pelvic denticle area of the mature female of Fig. 17; B × 3.4, portion of left pelvic denticle area of the mature female of Fig. 16B.

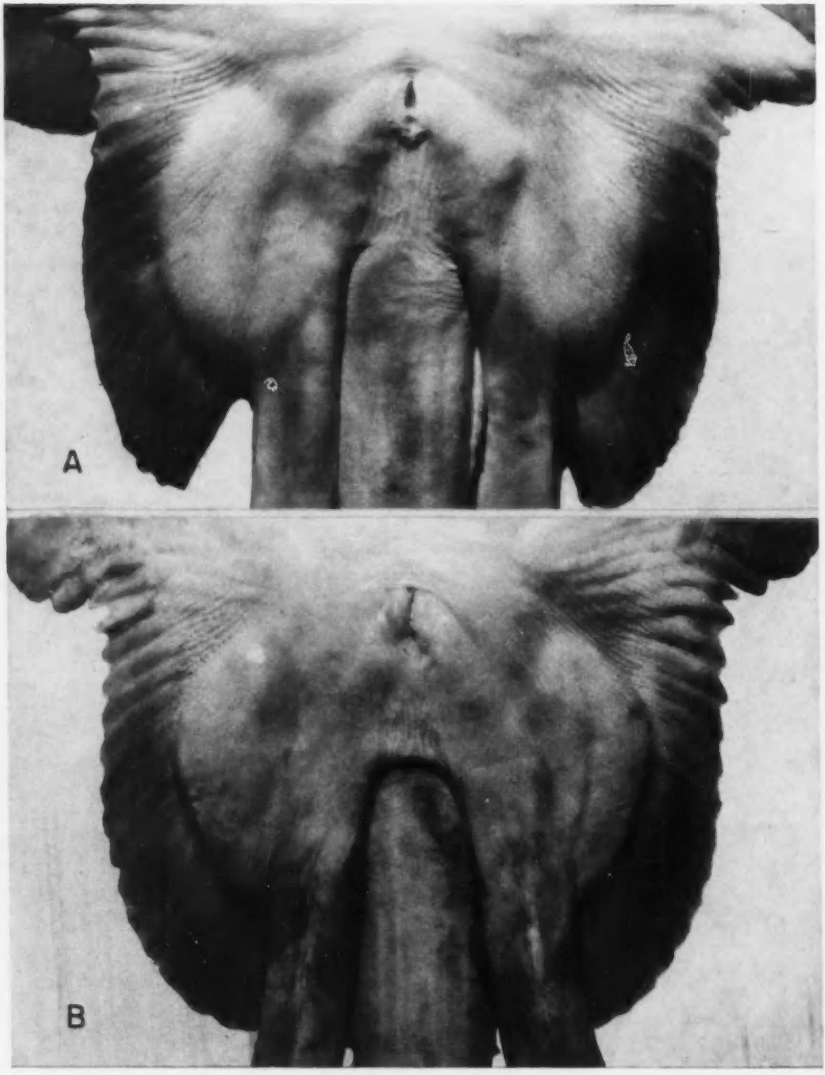

FIG. 19. *Raja ocellata* in ventral view × 0.4, showing location of the patches of pelvic denticles in males.

	Total length	Sex and maturity	Tooth count		Locality	Depth	Date	Ship
			Upper	Lower				
	cm		*no.*	*no.*		*m*		
A.	88.5	M mature	75	77	Twillingate, Notre Dame Bay, Nfld.	18–27	July 6, 1964	
B.	84.5	M mature	70	71	Trepassey Bay, Nfld.	4–18	August 11–13, 1964	*Investigator II*

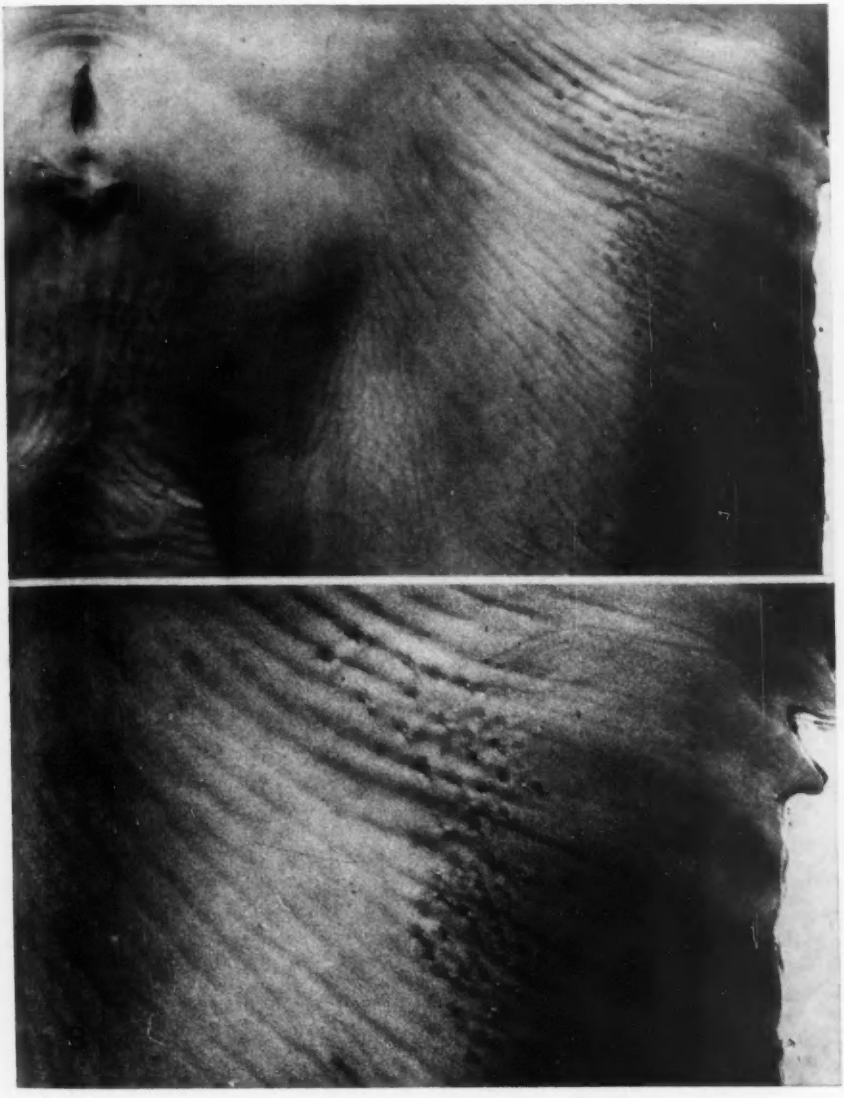

FIG. 20. *Raja ocellata* in ventral view, A, natural size, B × 1.8, showing the left pelvic denticle patch of the male of Fig. 19A in more detail.

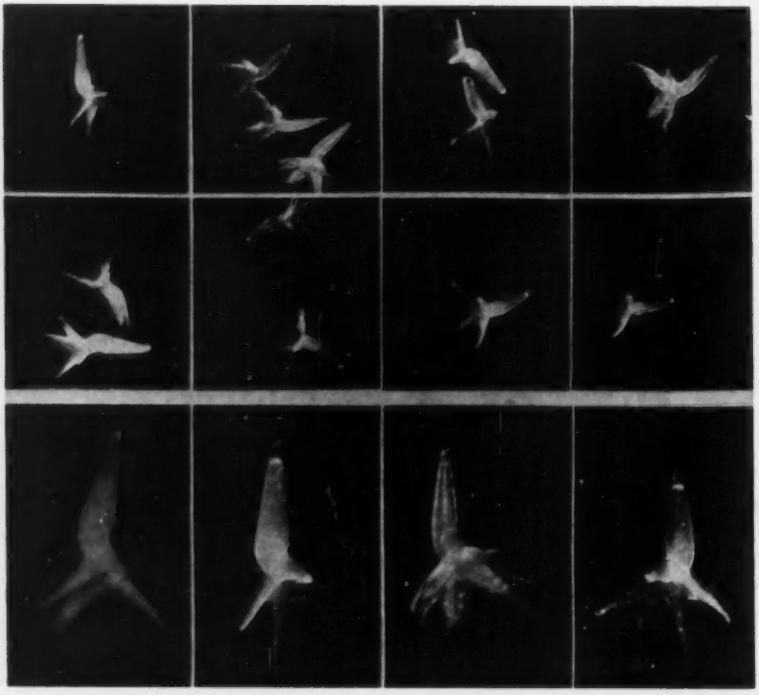

FIG. 21. Lateral view of the ventral pelvic denticles, upper two rows × 15 (same magnification as in Fig. 22 and 23 for *R. ocellata*), lower row × 30, of *Raja erinacea* from Georges Bank and the Nova Scotian Shelf, showing the spine which protrudes through the skin and the 4–5-rayed bases which are embedded in the skin.

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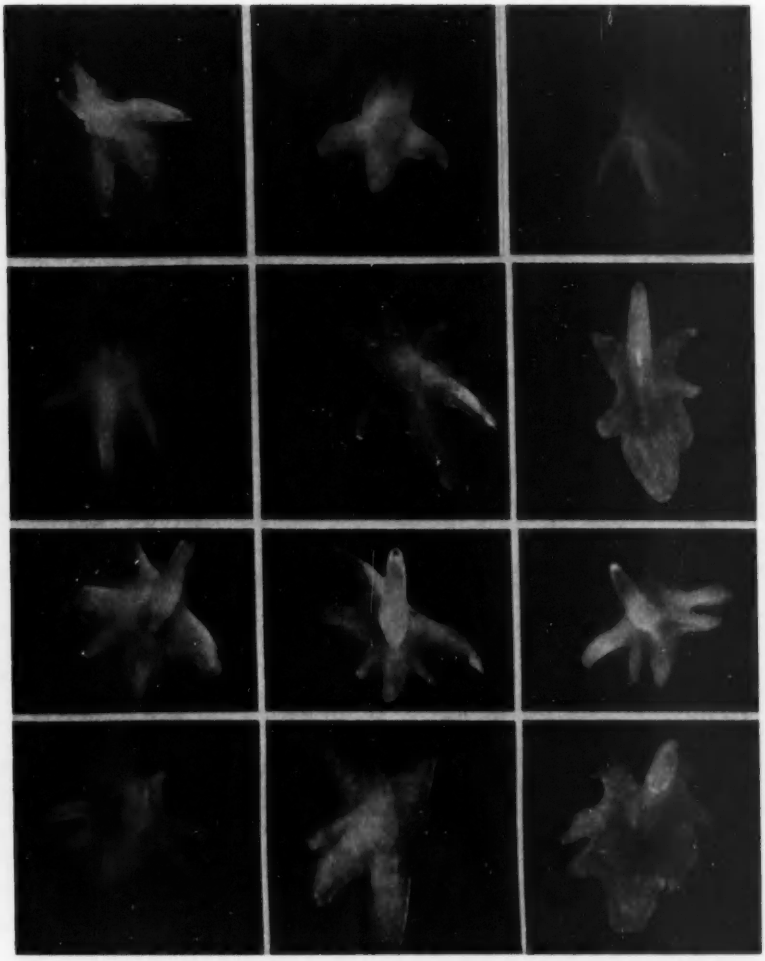

FIG. 22. View of outer surface of ventral pelvic denticles × 15, of *Raja ocellata* from the Newfoundland inshore area, showing the spine which protrudes through the skin and a variety of forms of 4–7-rayed bases which are embedded in the skin.

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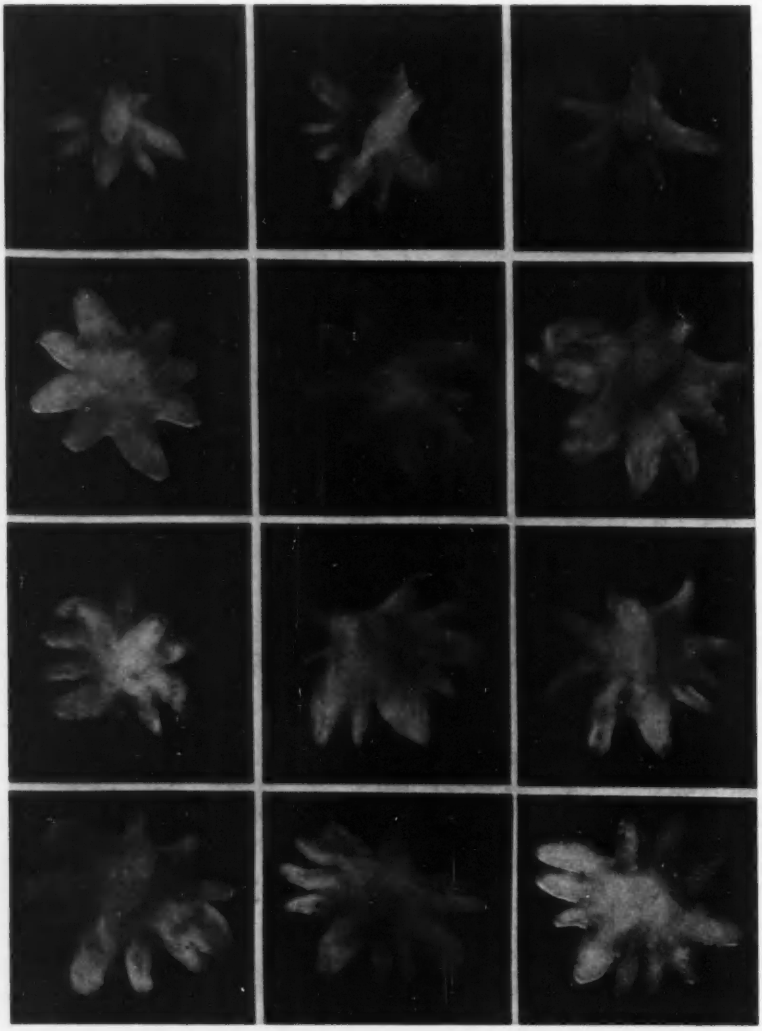

FIG. 23. View of outer surface of ventral pelvic denticles × 15, of *Raja ocellata* from the Newfoundland inshore area, showing the spine which protrudes through the skin and a variety of forms of 7–11-rayed bases which are embedded in the skin.

Nova Scotian Shelf, the remainder being from Georges Bank. Some mature females from Georges Bank showed a development of denticle patches posteriorly and laterally on the pelvics greater than in any of the three mature *erinacea* examined from the Nova Scotian Shelf, but the small number of individuals examined from the Nova Scotian Shelf cannot be expected to provide the complete range of development of these denticle patches.

FEMALE *Raja ocellata*. The earliest appearance of the pelvic denticles in immature and early mature female *ocellata* with small cloacal openings (Fig. 15A,B,C) is not in the position described for *erinacea* at the base of the pelvic fins near the posterior axils of the pelvics and posterior to the cloaca, but occurs more laterally on the median lateral half of the pelvics. The denticle patch is also more anterior and in its preliminary development has its strongest group of denticles opposite the cloaca and some of the denticle rows extend anterior to as well as posterior to the cloaca. Moreover, the earliest denticles are situated laterally in individual pits in the grooves between the rays of the pelvic fins rather than more centrally on the relatively smooth area near the bases of the pelvic fins.

In later stage mature female *ocellata*, usually with enlarged cloacal openings (Fig. 15D–18), the ventral pelvic denticle patch increases its area and extends posteriorly to pass beyond the posterior axils of the pelvic fins. The denticles still tend to develop in the grooves of the medial part of the lateral portion of the pelvic fin, but do not develop near the cloaca as in *erinacea* to cover the areas of smooth skin anterior to the axils of the pelvics and between the lateral grooved parts of the pelvic fins and the cloaca. In spite of the larger size of *ocellata* the pelvic denticles of the mature females are much less numerous and the denticle patches cover less area relative to the size of the fish than in *erinacea*.

Four immature female *ocellata* (29–39 cm) possessed no pelvic denticles. All other female *ocellata* (56 to 81–90 cm) possessed pelvic denticles. The patches tended to be large in females above 71 cm and especially in mature females, although a few mature females possessed only small patches (Table IV).

Female *ocellata* from coastal Newfoundland waters, the Nova Scotian Shelf, and Georges Bank all had these pelvic denticles of the same type and in approximately the same location.

MALE *Raja erinacea*. We have examined three mature and two immature male *erinacea* from the Nova Scotian Shelf and 28 mature and 10 immature male *erinacea* from Georges Bank but none possessed pelvic denticles (Table IV).

MALE *Raja ocellata*. In most mature male *ocellata* (Fig. 19, 20) a strong but small and somewhat triangular patch of pelvic denticles develops directly opposite the cloaca on the anterior lateral parts of the pelvic fin and extends back along the pelvic fin, tapering off to a sharp angle posteriorly along the outer edge of the anterior part of the raised kidney-shaped siphon sac of the

clasper. In the specimens of mature male *ocellata* that we have seen the denticle patch does not extend as far posteriorly on the pelvic fin as in the mature female *ocellata*.

Pelvic denticles were absent in a small immature 38-cm male *ocellata*. Only two denticles were present on the left pelvic fin and none on the right pelvic in an immature 50-cm male, but denticles were absent on a very large 95-cm male which was immature but close to sexual maturity. Pelvic denticles were also absent in two large mature male *ocellata* but were present in 10 mature males, with strong patches (relative to those of males) in nine of these (Table IV).

Physical Appearance

Raja erinacea. In *erinacea* the bases of the pelvic denticles are not deeply seated. The covering layer of epidermis is readily removed and the skin digested by a strong solution of potassium hydroxide and the denticles are separated out from the flesh with very little injury. In this species the pelvic denticles are very numerous and small and usually possess a 4-rayed base. A small percentage of these denticles have a 5-rayed base (Fig. 21) and a much smaller percentage a 6-rayed base.

The following remarks are based on the examination of the extracted pelvic denticles from eight mature female *erinacea*, six from Georges Bank and two from the Nova Scotian Shelf. From each of these a large number of pelvic denticles (approximately 100) was extracted and examined for variation. The estimated percentages with 4-rayed bases ran from about 95 to 99.5. (These are only rough estimates as exact counts were not made.) There was, however, a distinct difference between individuals in the percentage of pelvic denticles with bases of more than 4 rays. In the pelvic denticles with 4-rayed bases one of the basal rays is shorter than the others and the external spine leans in the direction of (toward) the short basal ray. In all cases the basal rays are cleanly cut and relatively sharply pointed and do not form a broad basal plate. In denticles with 5–6-rayed bases, sometimes the short ray is divided either at the tip or deeply enough to form 2 short rays or the additional ray or rays may be long.

Raja ocellata. In *ocellata* the bases of the pelvic denticles are more deeply seated and the skin and the covering epidermal layer are much thicker than in *erinacea*. It is thus considerably more difficult than in *erinacea* to separate the pelvic denticles from the flesh cleanly and without injury to either the basal rays or the spine of the denticle. It is possible, however, to extract these denticles by digesting the skin with a strong solution of potassium hydroxide. In a trial with one specimen, pelvic denticles in excellent condition were obtained by allowing the skin containing these denticles to rot in water.

The following account is based on the examination of extracted pelvic denticles from three mature male *ocellata*, 84.5–92.2 cm long, and four mature and one immature but maturing female *ocellata*, 78.3–82.2 cm long, from Trepassey Bay, Newfoundland, and one mature male *ocellata*, 88.5 cm long, from Notre Dame Bay, Newfoundland. In *ocellata* the pelvic denticles are

much less numerous and, even allowing for the much larger size of the fish, the denticles, especially their bases, are relatively much larger than in *erinacea*. The denticles in one individual may range from those with small 4-rayed bases, usually not as sharp-rayed as in *erinacea*, to those with large broad bases with 11 or possibly more rays which are usually rounded at the tips rather than sharp-pointed (Fig. 22, 23). There is a very great variety of shapes and sizes in the same and in different individuals. The oldest and best-developed pelvic denticles are large with a broad flat basal plate usually with a larger number of rays. The newly developing pelvic denticles, situated mainly laterally, posteriorly, and anteriorly on the outside of the pelvic patch and in intermediate rows between the rows of larger and older denticles of the deepest grooves, are smaller, with smaller bases and usually less basal rays. However, a moderately broad base may occur with as few as five or six basal rays. These statements are generally true for both male and female *ocellata* possessing pelvic denticles, but the mature female has a much larger patch of these denticles than the male and is likely to possess pelvic denticles showing a greater variety and range of bases and basal rays. The spines of the pelvic denticles of *ocellata* are often worn down at the tip, presumably from the movement of the pelvic fins in contact with a rough bottom. The spine usually leans backward over the space between two basal rays of the denticle which are generally set at a wider angle and are often shorter than the other rays. This situation is somewhat similar to that in the occasional *erinacea* with a divided short basal ray. Sometimes the spine leans backward over a single basal ray or another ray develops between or as an offshoot from the original pair. The base of the denticle is roughly bilaterally symmetrical. Usually the ray that the spine leans away from can be considered as a main or central or principal ray on each side of which pairs of rays are balanced. The two rays in each individual pair have approximately similar shapes. Sometimes one of these rays of a pair may be split to form two rays or possess a smaller accessory ray.

The above statements are generally correct for the five female and four male *ocellata* from which pelvic denticles have been extracted. However, only parts of the denticle patch of each species have been extracted and examined. In some individuals the greatest number of basal rays observed was as low as 7–8, in others as high as 10–11 but this range might be narrowed by extracting and examining the whole patch of pelvic denticles. The range and variety of bases in pelvic denticles might form an interesting study for individuals of *erinacea* gathered from various areas and in *ocellata* between areas and between sexes.

DISCUSSION AND CONCLUSIONS

Of the presently recognized differences between *R. erinacea* and *R. ocellata* none is absolute. Although eye spots on the posterior parts of the pectorals occur more commonly in *ocellata*, they have been shown to be present and distinct in some *erinacea* from the Nova Scotian Shelf and present but faint in occasional *erinacea* from Georges Bank. The tooth counts, high in

ocellata and low in *erinacea*, although not overlapping in the area generally, are highly variable and possibly subject to environmental influences. The counts may overlap slightly throughout the distribution range or the size range although there is no definite evidence for this at present. The differences between the small sizes at first sexual maturity and the small final sizes in *erinacea* and the larger sizes in *ocellata* are presumably also subject to environmental influences. In the Newfoundland area cod of the southern Grand Bank are 20 cm or more longer at first sexual maturity than Labrador cod. In the thorny skate those of the southern Grand Bank are considerably longer at first maturity than those of Labrador.

The division into species on the basis of tooth count and size at sexual maturity also cannot be objective; all skates of the *erinacea-ocellata* type with a high tooth count are called *ocellata*, the confidence in the decision being great if the skates are large, and all skates of this type with a low tooth count are called *erinacea*, the confidence being great if the skates are mature at a small size.

The differences in the pelvic denticle arrangement and appearance which we have shown in the larger females of the two species, which are now separated by tooth count and size at maturity, provide the first clear and completely objective anatomical differences. The absence of these pelvic denticles in all male *erinacea* and their presence on the pelvic fins in most large males of *ocellata* provide another readily recognizable difference between the two species. These differences should be of value in clearing up doubtful cases such as that observed by Richards *et al.* (1963) for the very doubtful *erinacea* from the Miramichi Estuary and will provide a solid basis from which positively identified *erinacea* and *ocellata* tooth counts and sizes at sexual maturity can be obtained for the larger immature and the mature fish of these two species.

Garman (1875) said that on each side of the vent, extending back upon the ventrals, adult females of the Rajae have close-set patches of shagreen-like scales. These seem most prominent in skates about to deposit their eggs. They are not found in the males. A similar statement is made for *Raja erinacea*. For *Raja ocellata* variety *diaphana*, Garman said that the females have the small scales around the vent.

These statements by Garman seem to refer to the same little spines that we have described as ventral pelvic denticles. His general statement on these denticles in the Rajidae is more descriptive of the condition in *erinacea* than it is for *ocellata*. If he is indeed referring to the same structures, his description for *ocellata* is incorrect since the denticles are not near the cloaca in this species but situated more laterally on the pelvic fins (ventrals). Also Garman did not note the presence of pelvic denticles in male *ocellata* nor did he note the differences in the distribution and form of these spines in the two species.

Regarding Garman's description of these pelvic denticles as occurring generally in adult females of the *Raja* group, we have examined numerous mature female and male *Raja senta*, *Raja radiata*, *Raja fyllae*, several large (over 130 cm) male and female *Raja spinicauda*, and one mature and one large

maturing *Raja jenseni* and no pelvic denticles were found. However, in barn-door skates, *Raja laevis*, from Georges Bank, although four immature females (38–47 cm) and two immature males (49 and 51 cm) possessed no ventral pelvic denticles, an immature female of 61 cm total length possessed the beginning of a small patch of pelvic denticles on each side of the cloaca as in *erinacea*. This skate was very immature, with egg diameter less than 0.1 cm and the combined weight of two shell glands less than 0.1 g, and it can thus be fairly well assumed that mature barn-door females possess well-developed patches of pelvic denticles. Garman (1875) does not mention these denticles in his account of *R. laevis*.

By one of the strange lapses which occurs occasionally in biology the presence of these pelvic denticles in *erinacea* and *ocellata* appears to have been lost sight of subsequent to Garman's (1875) paper. Garman himself in his paper "The plagiostomia" (1913) does not mention the pelvic denticles in his descriptions of *erinacea* and *ocellata*. Similarly Bigelow and Schroeder (1953) make no mention of them for *erinacea* and *ocellata*, but they presumably refer to them in their description of large females of *R. laevis* as being more or less prickly ventrally on the anterior parts of the pelvics.

Garman (1875) thought that these patches of ventral pelvic denticles ("shagreen-like scales") served as a protection from the claspers of the male. This might be a reasonable assumption from their location on the soft tissue on each side of the cloaca in mature female *erinacea* but would not provide an explanation for their presence further out on the pelvics in female *ocellata* or for their presence anteriorly on the pelvics in male *ocellata*. It may be more reasonable to assume that these pelvic denticles may have some excitory action on the opposite sex during copulation.

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Effect of Temperature on Mortality and Rate of Development of the Eggs of the Windermere Char (*Salvelinus alpinus*)[1]

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ABSTRACT

Rate of development and mortality of eggs of the Windermere char (*Salvelinus alpinus willughbii*) were investigated. Excessive mortality occurred at temperatures above 8 C, total mortality above 12 C. Rate of development varied with the water temperature, eggs taking on an average 45 days to hatch at 10 C and 95 days at 4 C.

INTRODUCTION

Teleost eggs hatch within a limited temperature range which varies for different species. Within this range of temperatures, eggs develop faster with warmer water. Ainsworth (1859) demonstrated this fact with American brook trout, and his results were confirmed by Embody (1934), who also examined the effect of water temperature on development rate of brown trout (*Salmo trutta*), lake trout (*Salvelinus namaycush* Walbaum), and rainbow trout (*Salmo gairdneri*) eggs. This subject was reviewed by Hayes (1949).

In a previous paper, Swift (1964) showed that since the Windermere char (*Salvelinus alpinus willughbii*) grew well in water temperatures between 12 and 16 C, the naturally occurring water temperatures encountered by this fish could not be regarded as a factor limiting their geographical distribution. It was therefore decided to investigate the effect of temperature on percentage mortality and development rate of eggs of this fish. There are, in Windermere, two distinct breeding populations of char, one population spawning in shallow water in autumn, and the other in deep water in spring (Frost, 1951). The effect of temperature on eggs of both populations was examined.

METHODS

Ripe fish were netted on the spawning grounds and six females were stripped of their eggs into separate polythene containers. Each batch of eggs was fertilised with milt from two males. Water was added after fertilisation; the eggs were allowed to swell before being transported to the laboratory. Approximately 50 eggs from each female were placed in perforated polythene containers floating at the water surface in aquaria. Throughout this experiment, except for brief inspection periods, light was excluded. The aquaria

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were supplied with running water and continuously aerated. At the start of each experiment the temperature of the aquaria was the same as that in which the fish were spawning. After the eggs were in the aquaria, temperature controls were set to each of the following temperatures: 2, 4, 6, 8, 10, 12, 14, 16 C; the water attained selected temperature during the course of a few hours. During the experiment, the water temperature was held within 0.1C of the selected temperature. Daily records were kept of number of dead eggs or hatched alevins in each tank.

RESULTS

A fault in the 2 C aquarium cooling system permitted only the start of hatching of the autumn spawning char to be recorded for this temperature. Various mortality rates for eggs at different temperatures (Fig. 1) showed that temperatures above 8 C resulted in very heavy mortality. At 12 C, none of the spring spawning char eggs, and only 3% of the autumn spawning char eggs hatched.

Deaths occurred randomly throughout the course of development among eggs developing at 4, 6, and 8 C, but eggs developing at higher temperatures showed a definite mortality pattern. This pattern is shown for eggs of autumn-spawning fish in Fig. 2. The majority of deaths occurred at two separate stages of development. The first stage at 5–15 days after fertilisation depending on the water temperature, and the second stage coincided with hatching.

Total mortality of the eggs at 8 C was only 15% and the majority of these deaths occurred at hatching. With increasing water temperature, a progressively larger proportion of eggs died at the earlier stage of development; at 14 C all eggs died at this early stage.

There was no difference between the hatching times of eggs of the two populations of char at different water temperatures (Fig. 3 and Table I).

Embody (1934) showed that the period from commencement to completion of hatching in rainbow trout varied in length with water temperature. For example 394 eggs took 14 days to hatch at 5.1 C whereas, at 17.6 C, 600

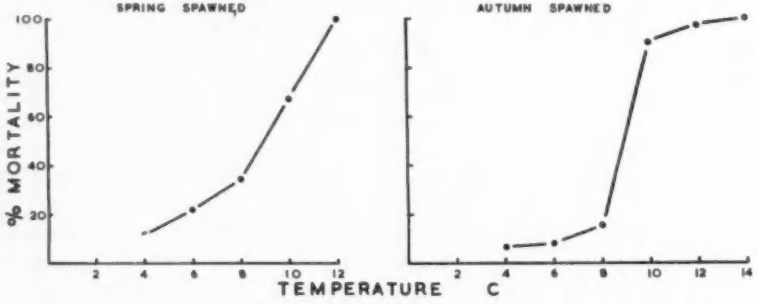

FIG. 1. Total number of dead eggs expressed as a percentage of eggs at the start of experiment plotted against the water temperature.

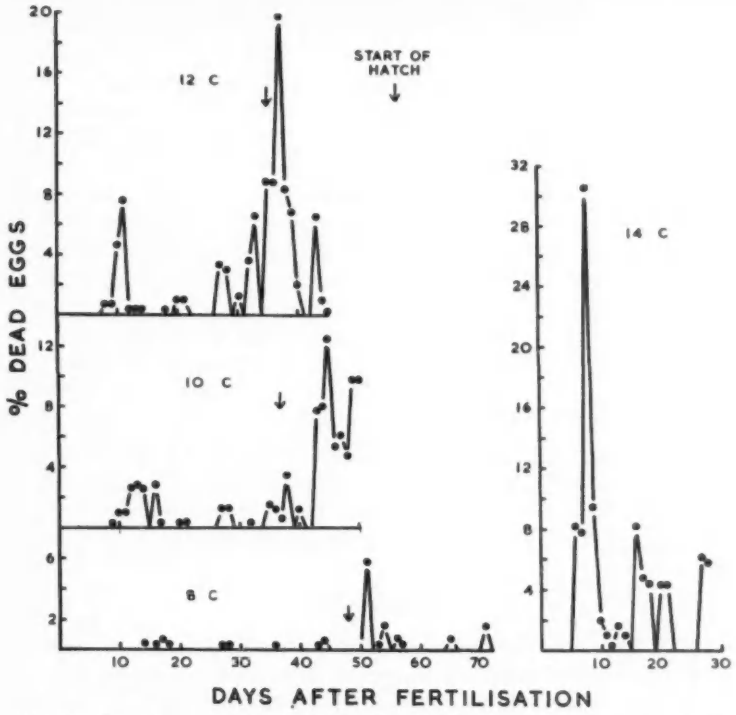

FIG. 2. Number of eggs dead each day after fertilisation expressed as a percentage of eggs at start of experiment.

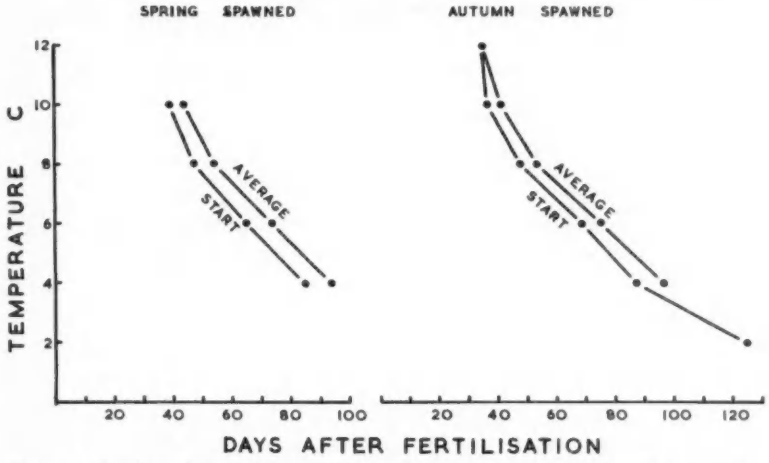

FIG. 3. Number of days from fertilisation to hatching of eggs for various water temperatures. The shortest and the average times taken are shown.

TABLE I. Hatching time at various temperatures.

Temperature	Average time (days) ± S.E. mean	
	Autumn	Spring
4	96.7±1.0	94.8±0.2
6	75.7±0.2	74.3±0.2
8	53.7±0.3	54.7±0.2
10	41.3±0.3	44.6±0.2
12	35.5±0.2	

eggs were all hatched in 3 days. Table II shows that this variation with temperature of hatching period did not occur in char eggs. Except for eggs of the autumn-spawning fish incubated at 10 C and 12 C from which only 32 and 10 alevins, respectively, emerged, the time taken for completion of the hatch varied between 21 and 38 days with little apparent relation to temperature of incubation.

DISCUSSION

The two stages during the development of the char eggs at which maximum mortality occurred have been observed in the development of the eggs of other salmonid species. Steuert (1906) found that eggs of brown trout taking 50 days to hatch were most susceptible to shock 10–17 days after fertilisation. Hayes and Armstrong (1942) found that there were two periods of maximum mortality in the development of eggs of salmon (*Salmo salar*),

TABLE II. Hatching period at various temperatures.

Temperature	Hatching period (days)	
	Autumn	Spring
4	38	20
6	21	26
8	21	30
10	7[a]	22
12	2[b]	–

[a]32 alevins.
[b]10 alevins.

the first period corresponding with the closure of the blastopore and the second with hatching.

Hayes (1949) suggested that, particularly at higher temperatures, deaths occurring immediately before hatching may be due to asphyxiation because the rate of diffusion of oxygen through the capsule was insufficient to meet the needs of the well-developed embryo. Gray (1928) showed that in trout eggs the temperature coefficient of the hatching mechanism was higher than that of other processes of development, resulting in precocious hatching of eggs at higher temperatures. In this experiment, the heavy mortality among eggs in the warmer water during the early stage of development could have been due to asphyxiation, however, those embryos which died at the later stage of development did so at the point of hatching, or immediately after they had hatched, suggesting that it was precocious hatching and not a lack of oxygen which was responsible for their deaths.

Under the conditions of this experiment, eggs of the Windermere char did not achieve more than a 32% hatch in temperatures above 8 C. It is apparent that, although temperatures normally encountered by these fish will not affect their geographical distribution (Swift, 1964), the low upper lethal temperature of their eggs, when compared to that of other salmonids, very probably will do so.

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Sedimentation in a Salmon Stream[1,2]

By S. Philip Shapley[3] and Daniel M. Bishop

ABSTRACT

Sediment was artificially added to a small southeastern Alaskan salmon stream. Observations in sedimented and control riffles indicate that the amount of sediment settling to the stream bottom decreases exponentially with distance downstream. The dissolved oxygen content of intragravel stream water remained high in sedimented riffles. The added sediment was removed from stream-bed gravels by fall freshets and floods.

INTRODUCTION

Ample evidence has been presented to demonstrate the adverse effects of stream-bed sedimentation on the survival of salmonid embryos and larvae in spawning beds (Shaw and Maga, 1943; Andrew and Geen, 1960; Cordone and Kelley, 1961). Sediment renders the redd area less permeable (McNeil and Ahnell, 1964), and reduces porosity of stream-bed gravel, thereby diminishing flow (Fair and Hatch, 1933).

Sediment is generally a product of geologic erosion such as landslides and stream-bank cutting. Mining sediment, sand, and organic detritus from logging and road building (McNeil and Ahnell, 1964) proceed from erosion caused or accelerated by man. Sediment settles on the stream-bed from the flowing water mass, in which it is transported in suspension.

An understanding of sedimentation of spawning areas and of its control can clarify some ecological aspects of natural and man-caused changes in the stream environment of the pink (*Oncorhynchus gorbuscha*) and chum (*O. keta*) salmon.

This study sought: (1) to determine the distribution of suspended sediment settling out of the stream; (2) to observe the effect of sediment on the composition of stream-bed gravels; and (3) to learn the conditions under which deposited sediments may be removed. These factors are linked to salmon production.

MATERIALS AND METHODS

The study was conducted in Maybeso Creek, Prince of Wales Island, Alaska, 45 miles west of Ketchikan. The main rock types in the drainage basin are argillite, graywacke, and related slates and conglomerates. These rocks are easily weathered. The timber was clear-cut on about 30% of the 20.5-sq mile drainage basin of Maybeso Creek. Both pink and chum salmon

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use the stream. The peak observed run for pink salmon is 5500; for chum salmon — 5200. The locations of riffle sample areas and the sediment source are shown in Fig. 1.

Sediment was produced by hydraulically mining a stream-side alluvial sediment deposit. Production began on August 10, 1961, and continued for 10 working days through August 22.

The composition of stream-bed materials was measured in four comparable 20 ft × 40 ft riffle areas. Sediment was introduced into the stream at a point upstream from three of the riffles, to determine the sediment movement downstream. The three riffles downstream from the point of the introduction of sediment will be referred to as treatment riffles A, B, and C, and the one upstream as the control. The composition of stream-bed materials was measured immediately after exposure to suspended sediment, and again after flooding.

The amount of suspended sediment in the stream was determined with depth-integrated samples of approximately 300 ml taken with a U.S. DH-48 hand sampler (U.S. Inter-Agency Committee on Water Resources, 1959) at intervals across the stream cross-section. Sediment was filtered from the samples by glass fiber filters in Gooch crucibles under a vacuum. Size composition of the suspended sediment was not determined.

Suspended sediment samples were taken from stream sections at distances of 530, 1344, 1935, 2157, 2537, 2965, 3203, and 4016 ft below the sediment source. At the sample section 530 ft below the sediment source, a temporary recording stream gage was located for determining flow volume in estimating the weight of suspended sediment produced. Suspended sediment was measured at the various sampling stations to provide a measure of drop-out rate as a function of distance downstream from the sediment source. In one series of samples, a float was set adrift on the stream as an index of current flow; the suspended sediment in a particular portion of the stream water was measured as the float arrived at each sampling station. The other series of samples was taken at random, based on the assumption of a constant rate of sediment introduction to the stream.

A suspended sediment sample for a particular time and place was composed of three subsamples in the stream cross-section. Subsamples were processed individually.

To measure the effect of sediment on the stream-bed, gravel composition samples 6 inches in diameter and 6 inches deep were extracted at 25 points in each of three riffles below the sediment source and in one riffle above it. The technique used is similar to that developed by McNeil and Ahnell (1964), except that a plunger was used instead of a cap (Koo, 1964). Samples were taken in July 1961 (before sedimentation), late August 1961 (immediately after sedimentation), and June 1962 (after large floods).

Each sample was wet-sieved to determine the volume content of 10 size classes of material. The largest size was retained by a 1-inch sieve and the smallest passed a 0.104-mm sieve. The latter material (called pan size) was

collected from the base of a large funnel after 10 min of settling wash water. Differences in the amount of fine material (material passing a 0.833-mm screen) within the stream-bed riffle before and after sedimentation were used to express the amount of sediment accumulated.

A permanent stream-height recorder, located about 3 miles downstream from the lowest treatment riffle, was used to measure stream-flow.

To determine erosion or sediment deposition in the stream-bed during flood flows, 14 columns of six perforated ping-pong balls were buried in each study riffle. Balls were placed through hollow drive pipes at depths of 1, $2\frac{1}{2}$, 4, $5\frac{1}{2}$, 7, and $8\frac{1}{2}$ inches below the stream-bed surface. Each column was marked with a plastic cord to aid relocation. The loss of balls indicated the depth of stream-bed movement.

Water samples for dissolved oxygen determination were collected from the stream-bed, to obtain an indirect measure of effect of accumulated sediment on salmon egg survival. They were drawn through driven standpipes at depths of 6–9 inches below the stream-bed surface, and were analyzed by the unmodified Winkler method.

RESULTS

Suspended Sediment Production and Measurement

Sediment was introduced into the stream for about 70 hr during the 10 days in the period August 10–22. About $5\frac{1}{2}$–6 tons of suspended sediment passed sample point 1 (Fig. 1). During the 10-day period the average suspended sediment concentration was 55 ppm at treatment riffle A, and the average streamflow, about 12 ft^3/sec. The weather at this time was sunny and dry, producing low streamflows. Suspended sediment composition averaged 27% organic matter, 73% inorganic. Sediment was deposited on the stream-bed as far downstream as treatment riffle C, 1935 ft below sediment source (Table I).

Two days after the introduction of sediment was completed, the first fall rains arrived. The resultant moderate streamflow of 670 ft^3/sec removed the stream-bed sediment coating before post-sedimentation sampling could begin. The greater part of some 1–2 tons of sediment that had accumulated in the pool between treatment riffle A and the sediment source was flushed downstream.

The mean sediment values for three sets of suspended sediment samples taken at locations 2 through 8, shown in Fig. 1, are plotted in Fig. 2 to show the relationship of suspended sediment concentration to distance from the sediment source while sediment was being added.

A regression was calculated for each of three sampling dates of the proportions

$$\frac{\text{organic suspended sediment concentration}}{\text{inorganic suspended sediment concentration}}$$

versus distance. For two of the

three dates, the regression was nonsignificant, but for the third it was significant at less than the 0.005 probability level. On this date (August 21) suspended inorganic sediment concentration relative to organic sediment concentration decreased faster with distance.

Stream-Bed Gravel Composition

Stream-bed gravel composition was measured during three periods: prior to sedimentation, after sedimentation (a moderate freshet, and some spawner

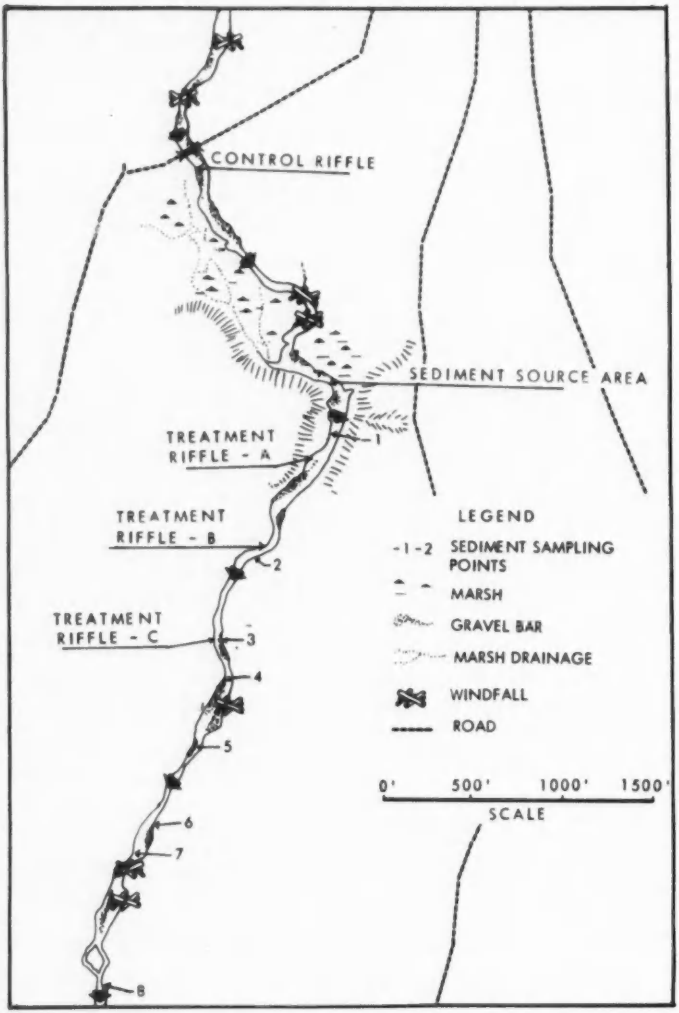

Fig. 1. Sediment study areas.

TABLE I. Volume[a] of stream-bed material 0.833 mm and smaller in four riffles, before and after sedimentation, and after a flood.

Time	Control riffle	Treatment riffle A	Treatment riffle B	Treatment riffle C
	%	%	%	%
Before sedimentation	7.8	12.4	7.8	11.6
After sedimentation and a moderate freshet	5.3**	16.1*	8.4	10.1
After sedimentation and a large flood	4.2	12.1	6.3	–

Probability that the change in gravel composition from previous sample is due to random variation:
* $P < .05$
** $P < .01$.

[a]Expressed as a percentage of total volume.

activity occurred before the "after-sedimentation" measurements could be taken), and after a major flood. In our analysis we considered only material passing through the four smallest screen sizes of sieves: (a) material 0.833–0.417 mm; (b) 0.417–0.208 mm; (c) 0.208–0.104 mm; (d) < 0.104 mm.

In treatment riffle A, the volume of material passing through the 0.833-mm screen (size classes a, b, c, d) increased significantly ($P < .05$) between the first and second measurements (Table I), and nonsignificantly in riffle B. There was a nonsignificant decrease in riffle C and a highly significant ($P < .01$) decrease in the control riffle. The change in the control riffle indicates that moderate freshets clean the gravel of fine materials in natural streams.

The volume of stream-bed material less than 0.833 mm in diameter decreased between the second and third measurements. The change in treatment

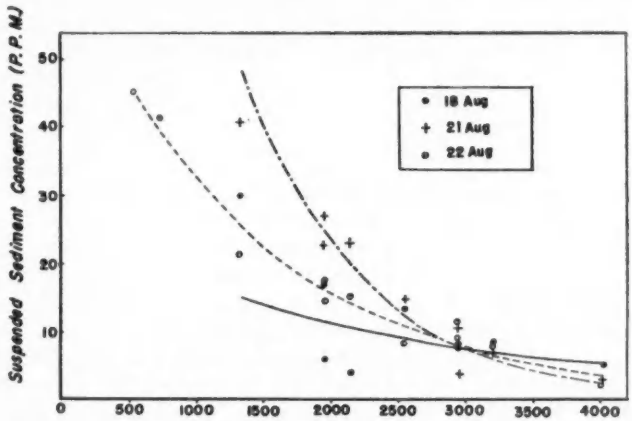

FIG. 2. Change in *total* suspended sediment concentration with distance from sediment source.

riffle A was significant at $P < .05$ level. Treatment riffle B showed a nonsignificant decrease. Measurements were not taken in treatment riffle C during the third period. The decrease in the control riffle was nonsignificant.

At the same time very few ping-pong ball columns were relocated. From 14 columns of ping-pong balls buried in each study riffle, three columns were the most that were recovered from any riffle. Other columns were presumably swept away by scouring, or were buried under new gravel deposits.

Dissolved Oxygen

Dissolved oxygen in the stream-bed riffles remained at near saturation levels immediately after sedimentation (Table II).

DISCUSSION

Settling of Suspended Sediment

Inorganic sediment apparently settles to the stream-bed faster than organic material, presumably because of the difference in specific gravity. Undoubtedly, much organic material from the sediment source settled to the stream-bed during low flows, but was probably flushed and swept downstream by the first high flows of the fall season. This has been observed during the fall suspended-sediment sampling in streams in the Hollis area of Alaska; the first fall freshet will flush a higher percentage of organic sediment than the later flows. The present findings indicate that organic sediments are displaced downstream more rapidly than inorganic. This is fortunate, because decomposition of organic sediments draws upon the supply of dissolved oxygen in the stream. Upon reaching the estuary, organic and inorganic sediments fall to the tide flats.

Table II. Dissolved oxygen content[a] of stream-bed water in four riffles before and after sedimentation and a freshet.

Time	Control riffle		Treatment riffle A		Treatment riffle B		Treatment riffle C	
	Mean[a]	Sample size	Mean[a]	Sample size	Mean[a]	Sample size	Mean[a]	Sample size
July 28 Before sedimentation	94	24	85	25	91	24	93	24
August 25 After sedimentation and 1 day after a moderate freshet	96	17	87	5	94	14	87	13
September 3 After sedimentation and 1 week after the previous observations	97	21	95	24	98	20	95	20

[a]Per cent of saturation.

A regression of the logarithm of suspended sediment concentration against distance demonstrated that suspended sediment levels decrease at an exponential rate (Fig. 2). Sediment sampling at Hollis, as well as in western Washington and Oregon (Barton, 1951; Fredericksen, 1963), shows concentration of suspended sediment in a stream as a logarithmic function of stream discharge. The trend toward the same rate of exponential decrease downstream during the three sampling periods reflects the stable flows between August 18 and 22.

Sediment deposition during the treatment phase of the study was described earlier. Deposition occurred in treatment riffle A when flow velocities at 0.4 ft above the stream bottom averaged about 0.325 ft/sec. The material was flushed out by the first freshet before it could be measured, but it appeared and felt like fine sediment.

During the flood of August 24, the flow produced velocities of around 3.44 ft/sec 1.2 ft above the stream bottom. This flow picked up sediments from the stream-bed, and swept larger silt and sand particles out of pools.

The data collected were insufficient to establish critical levels of flows and velocities required to move particles of specific size. The work indicates the need for knowledge of size, shape, and weight of sediment particles in southeast Alaska streams. More information on hydraulic parameters, such as stream-bed roughness, is needed for a quantitative determination of sediment problems in southeast Alaska.

Stream-Bed Gravel Shift

A statistically significant change in stream-bed composition extended more than 600 ft, but less than 1300 ft, downstream from the sediment source after the moderate freshet of August 24, 1961, and spawner activity. Flood flows unsettled the stream-bed in the first 2 weeks of October 1961. These high flows dislodged and cleaned out the fine materials, reducing them to pretreatment levels. The flow of October 13–14 was the greatest since gaging began in 1949. Large changes in the bed at this time were indicated by later ping-pong ball recoveries.

Thus it appears that high stream flows can largely determine the size composition of stream-bed material. Streams with low high flow:low flow ratios require less sediment load to make more or less lasting changes in gravel composition, compared with streams with high ratios. Maybeso Creek, for example, has a 14-year record peak flow ratio of 444.4:1. Fish Creek, near Ketchikan, with a ratio of 270:1 (U.S. Department of the Interior, 1962), may have a greater susceptibility to stream-bed composition change as a result of disturbance and sediment load.

The observed diminution of fine material in the control riffle bed may have been the result of redd digging (density very roughly estimated to be about 2 female chum salmon/100 ft^2). Observations of McNeil and Ahnell

(1964) and of Semko (1954) indicate that spawners remove fine particles and organic detritus from the stream-bed.

Effect on Salmon Production

Evidence is nearly conclusive that sediment within the stream-bed reduces the rate of intragravel water flow. Terhune (1958) describes permeability measurement by use of the Mark VI groundwater standpipe. McNeil and Ahnell (1964) have demonstrated that a 4% increase in material less than 0.833 mm in diameter in a Hollis area stream-bed (as apparently occurred in our treatment riffle A) lowered the coefficient of permeability of the stream-bed about four times. They conclude that salmon production in many southeastern Alaska streams is inversely related to percentage of stream-bed material that will pass a 0.833-mm screen.

Wickett (1958) shows that a fourfold decrease in permeability, in some permeability ranges, is associated with over a fourfold decrease in pink and chum salmon production. Cordone and Kelley (1961) indicated that increased stream-bed sedimentation adversely affected salmon production. The evidence of other investigators thus indicates that when fine material accumulates in the stream-bed, salmon production is reduced. Although permeability was not measured in our experiment, it is reasonable to think it was temporarily reduced by sedimentation in treatment riffle A (Table I).

Oxygen supply to salmon eggs or larvae may afford an equally satisfactory index to the effect of sedimentation on salmon productivity. Oxygen supply within the stream-bed is determined by (1) dissolved oxygen supply of intragravel water, (2) oxidation demands, and (3) intragravel flow velocity. The importance of these variables has been discussed by Alderdice *et al.* (1958), Shumway (1960), and Silver *et al.* (1963).

There were generally high levels of dissolved oxygen in the study areas prior to and immediately after sedimentation. Oxygen demands were evidently low, reflecting either little organic accumulation or sparse egg deposition or both. After sedimentation the rate of exchange between intragravel and stream water may have remained sufficiently high to supply oxygen demands.

SUMMARY

Three riffle areas — treatment riffles — 20 ft × 40 ft were located below a man-made sediment source. One riffle area — untreated control riffle — was upstream from the sediment. Each riffle area was examined for gravel composition change, dissolved oxygen change, and stream-bed stability from August 1961 to June 1962.

Five to 6 tons of suspended sediment passed over the first treatment riffle during the 10 days of treatment. Suspended sediment concentration decreased with distance, and inorganic sediment settled faster than organic.

A moderate-sized storm in late August flushed sediment from the stream-bed surface, and larger particles from the pool immediately downstream from

the sediment source. Remeasurement showed a significant increase in fine stream-bed material less than 0.833 mm in treatment riffle A, and a nonsignificant increase in treatment riffle B. Extremely high flows in October 1961 flushed the stream-bed, removing significant amounts of sediment materials deposited earlier by treatment from treatment riffle A and the control riffle. Poor recovery of perforated ping-pong balls indicated an unstable stream-bed over the fall–winter season.

The work of others led us to believe that sedimentation caused conditions which may reduce salmon production. This proved true, temporarily, for gravel composition changes, but untrue for intragravel dissolved oxygen levels. The dissolved oxygen level of intragravel stream water remained consistently high on the three sampling dates in 1961, reflecting either low oxygen demands or sufficiently high intragravel flow rates. Gravel permeability or intragravel flow rates were not measured.

ACKNOWLEDGMENTS

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Rancidity in Lean Fish Muscle. IV. Effect of Sodium Chloride and Other Salts[1]

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ABSTRACT

Sodium chloride accelerated rancidity in blended cod muscle at 0 C. This salt-induced rancidity was retarded by commercial antioxidants and chelating compounds. The active agent appeared to be the Na^+ rather than the whole salt or the Cl^-.

Other metal salts had similar pro-oxidant action on the cod muscle when used in relatively high concentrations (0.1 N and above). The relative activity, using metal chlorides, was as follows: Fe > Co > Cd > Li > Ni > Mg > Zn > Na > K. Ca and Ba had no effect.

Many of these "pro-oxidant" salts also had a strong antioxidant effect on the development of copper-induced rancidity in the muscle.

The relationship between TBA values and the type and intensity of odours is not the same for sodium chloride-induced and copper-induced rancidities. Some of the reasons for this have been discussed.

It has been suggested that one mechanism by which sodium chloride influences the rate of lipid oxidation in the fish muscle is by the changes it produces in the accompanying proteins.

INTRODUCTION

In spite of the fact that sodium chloride is one of the most widely used food additives, there still remain many puzzling questions concerning its relation to the development of oxidative rancidity in food products. The subject was reviewed briefly by Lea (1938), Watts (1954, 1962), Tsuchiya (1961), Michell and Henick (1962), and Lundberg (1962).

That salt does accelerate rancidity in some foods is an established fact, but the mechanism of its action has not always been clearly understood. Several different explanations have been advanced. Lea (1938) suggested that the effect was the result of trace amounts of heavy metals contaminating the salt. Banks (1937) found that salt accelerated rancidity in raw herring, but not after it had been cooked. He suggested that the heat-labile system involved heme proteins, and later (1944) postulated that the active catalyst was a combination of heme and fat peroxides. Coleman (1951) showed that salt accelerated oxidation of hemoglobin and myoglobin to the ferric form. This explanation was further strengthened by Lea (1935, 1936), Banks (1944), and Mabrouk and Dugan (1960), who, by different approaches, were able to show that sodium chloride had no direct effect on the oxidation of lipids in the absence of other organic pro-oxidants.

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There is also some evidence to suggest that salt may have a protective action against the oxidation of food lipids. Kilgore (1934) found that salt prevented oxidation of cottonseed oil emulsified with pectin and water and made up into mayonnaise. Chang and Watts (1950) also suggested that since salt is not absorbed at the interface between fat and water, dilute salt solutions brought into contact with unsaturated fat may actually retard oxidation.

From this accumulated evidence it would seem that pure sodium chloride has no direct effect on the oxidation of lipids but acts only on nonlipid components which activate the lipid oxidation. One exception to this viewpoint was the theory proposed by Hills and Conchie (1946) in which fat peroxide reacts with chloride ions, resulting in the formation of chlorine. The free chlorine thus formed brings about further oxidation of the fat.

Sodium chloride affects many of the autolytic changes normally occurring in muscle tissue (Pavlovskii, 1960), changing both physical and chemical characteristics of some nonlipid components of the muscle. Of particular interest is the ability of salt to denature actomyosin and other proteins in the muscle. Salt probably disrupts the lipoproteins or other complexes containing lipids (Dyer, 1953). These observations suggest that more than one type of reaction is involved in the effect of salt on development of rancidity.

With fatty fish there is abundant evidence to show that the addition of salt accelerates rancidity (Banks, 1937; Banks *et al.*, 1957; Tarr, 1944). Very little is known, however, of its action on the lipids in nonfatty fish, such as cod or haddock. Cardin *et al.* (1958) found that during the preparation of lightly salted Gaspé-cured fish 77% of the fatty acids from the phospholipids were set free. There was no evidence to suggest what mechanisms were involved.

One method of preserving lean fish is by incorporating high concentrations of salt into the flesh, followed by drying in air and exposure to bright sunlight. If salt induces rancidity, these would seem to be the ideal conditions. Dry salt cod and other salted lean fish do have strong characteristic odours and flavours, but rarely become rancid.

Experiments were carried out with three objects in view: (1) to determine whether salt affects the development of rancidity without the addition of any other catalyst; (2) to see whether salt affects the rate of development of copper-induced rancidity; and (3) to determine whether other common electrolytes behave in a manner similar to sodium chloride.

EXPERIMENTAL PROCEDURES

Unless otherwise stated, the fish used were Atlantic cod (*Gadus morhua* L.), trawler-caught, usually less than 4 days in ice and always in a good state of preservation. Methods for preparing and storing blended fish muscle and for measuring rancidity were given previously (MacLean and Castell, 1964). In brief, the fish muscle was blended with three times its weight of water and stored at 0 C. Development of rancidity was followed by measuring the thiobarbituric acid (TBA) values (optical density at 538 μmoles after reaction with TBA) and noting the accompanying off-odours.

The sodium chloride used in these experiments was certified ACS reagent grade, "analysed and found to contain 0.0000% iron and 0.0000% heavy metals." The other salts were all certified reagent grade. The stated concentrations of salt, or other ingredients, refers to amounts added to the blend and not to the muscle itself. The amounts are always percentage by weight.

Susceptible and Unsusceptible Fish Muscle

It had been found previously (Castell and MacLean, 1964) that cod muscle was not equally susceptible to copper-induced rancidity throughout the year. During late winter and early spring, the induction period was much shorter than during the summer months, suggesting increased concentrations of natural antioxidants in the muscle following the period of more intensive feeding. Unless these seasonal differences in the susceptibility of the muscle to lipid oxidation are taken into consideration, considerable confusion may result in the interpretation of experimental results. For this reason, care has been taken to record in each experiment whether it has been carried out with "susceptible" or "unsusceptible" muscle. In brief, a susceptible muscle is one in which 20 ppm Cu^{++} added to the blend will produce strong seaweedy or rancid odours, and TBA values above 0.3, after 24 hr at 0 C. An unsusceptible muscle is one in which no off-odours are produced and the TBA value remains below 0.15 during the same holding period.

EXPERIMENTAL

The first set of tests showed the effect of a range of sodium chloride concentrations between 1 and 30% on the pH and the subsequent development of rancidity in the blended muscle (Fig. 1). The pH decreased with increasing amounts of salt and almost leveled off at concentrations above 18 or 20%.

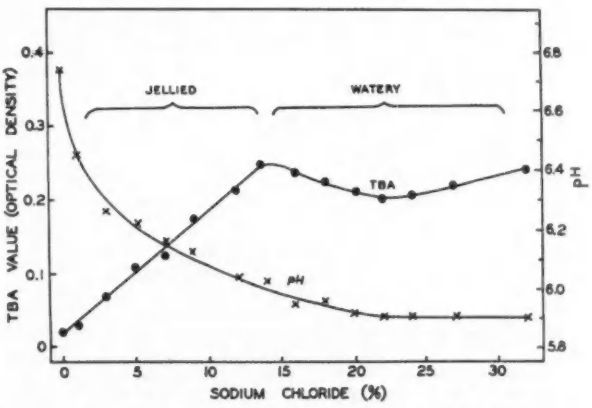

FIG. 1. Effect of sodium chloride concentration on pH and TBA values of blended cod muscle after 72 hr at 0 C.

These pH changes occurred as the salt was being mixed with the blend and showed little or no change during storage. In Fig. 2, it can be seen that the initial pH of the fish before the salt is added determined where the pH values level off.

TBA values showed no immediate change after adding salt to the fish muscle, but rose significantly during subsequent storage (Fig. 1). They increased with increasing salt concentrations up to about 14%, beyond which additional salt brought no further increases. These two phases of the TBA–salt curve correspond to the changes brought about in the physical condition of the blended muscle by the addition of salt. From about 1 to 14% salt caused the tissue to jell, as the proteins swelled by absorbing solution. At higher concentrations, the proteins lose this swelling tendency and synaeresis occurs, resulting in a watery mixture.

In most systems, decreasing pH accelerates the rate of lipid oxidation. It would be of interest, therefore, to know to what extent the activating effect of the salt on the development of rancidity was merely a result of its ability to lower the pH. To throw some light on this problem, two experiments were carried out. In the first, the salt content of a series of samples was kept constant at 12% while the pH was adjusted to give a range of 5.5–7.5 (using lactic

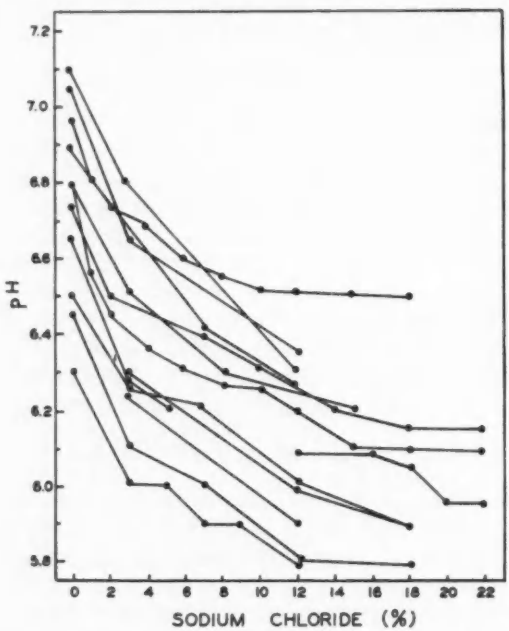

FIG. 2. Effect of sodium chloride on the pH of 14 lots of blended cod muscle having initial pH values from 6.2 to 7.1.

acid and sodium hydroxide solutions). Control samples, using fish muscle without added salt, were adjusted to the same pH levels. Decreasing the pH accelerated rancidity both with and without the salt, but the TBA values were higher where the salt had been added (Fig. 3A).

In the second test, the pH values were held constant and the salt concentration varied between 0 and 15%. There were three sets of tests: one buffered at pH 6.1; a second buffered at pH 7.2; and a third in which the pH values were unadjusted (Fig. 3B). When the pH was held at one level the TBA value still increased with increasing salt concentrations, but not to the same extent as when the pH was allowed to change. Thus, the salt itself affects the oxidation of the lipids in the blended muscle and this is further enhanced when the salt also lowers the pH.

In most of these tests, the addition of sodium chloride brought about the subsequent development of slight off-odours. With higher concentrations of salt the odours were perceptible after 24 hr and slowly intensified with longer storage periods. It was difficult to identify or characterize these off-odours, especially during the earlier stages. As the odours grew stronger, they somewhat resembled the seaweedy odours that are associated with the earlier stages of copper-induced rancidity. However, for the same TBA levels, the odours produced in the muscle by the addition of sodium chloride were very much less intense than those produced by copper. So far, none of the "rancid-fish-oil" or "linseed oil" odours accompanying the later stages of copper-induced rancidity have been encountered following the addition of sodium chloride.

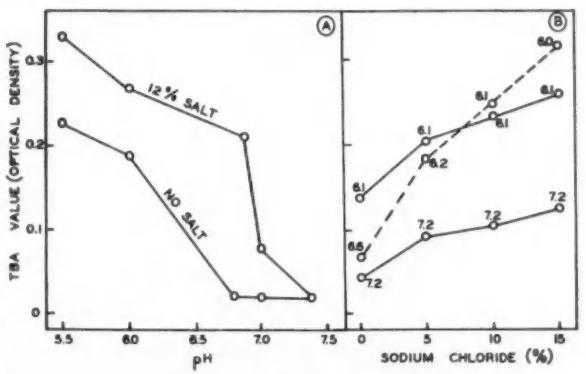

FIG. 3. A. Effect of pH between 5.5 and 7.5 on development of rancidity in blended cod muscle, with and without the addition of 12% sodium chloride. B. Effect of sodium chloride concentration on the development of rancidity in two series of blended muscle, one of which was adjusted to pH 6.2 and another to pH 7.2 after the salt had been added. A control set with unadjusted pH was used for a comparison.

Effect of Salt on Muscle Denatured by Heat and Frozen Storage

Figures 4A and 4B show the effect of a range of salt concentrations on the immediate pH levels and subsequent TBA values of heated (autoclaved) and unheated cod muscle. Salt depressed the pH values in both heated and unheated muscle, but the values were lower in the latter. Heating by itself raised the TBA values but also destroyed its capacity to bring about any further increase on storage.

With muscle from both fresh fish and fish that had been held in frozen storage until it showed signs of denaturation, the frozen stored fish had a slightly higher initial TBA value than the fresh fish. After the addition of sodium chloride the increase of TBA on storage was very much less with the fish that had been in frozen storage than it was with fresh unfrozen fish (Fig. 4). In fact, the picture is much the same with fish denatured by storage and the heat-denatured fish (compare Fig. 4A and 4C).

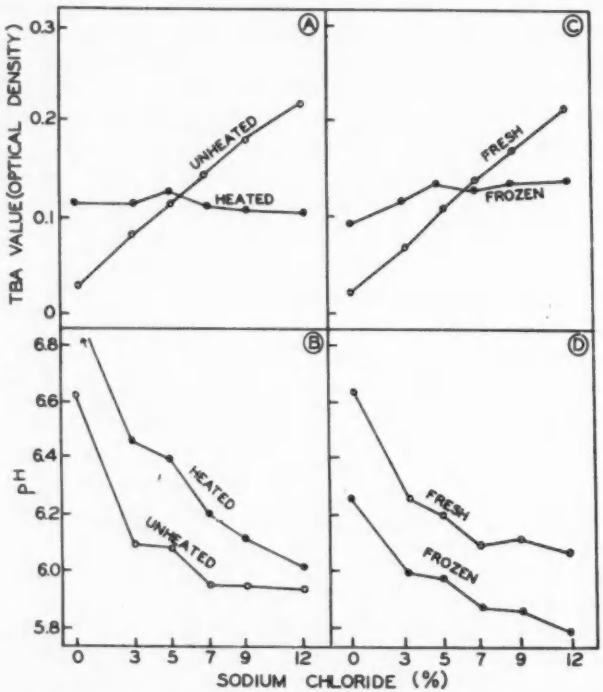

Fig. 4. A and B. Effect of sodium chloride concentration on TBA values and pH of blended cod muscle prepared from heated and unheated cod fillets. The values given are after 24 hr at 0 C. C and D. Effect of sodium chloride concentration on TBA values and pH of blended cod muscle prepared from fresh unfrozen and from frozen stored fillets. Values for 24 hr at 0 C.

Effect of Salt on Copper-Induced Rancidity

Sodium chloride was found to have either an accelerating or a retarding effect on copper-induced rancidity, depending upon the relative concentrations of Cu^{++} and NaCl. For example, using susceptible fish caught early in March, a series of tests was carried out with three different concentrations of salt in combination with three different copper concentrations and following four different storage periods (Fig. 5A–D). In the absence of both Cu^{++} and NaCl there was little or no change in the TBA values during the 168-hr holding period. As noted previously, the addition of salt without Cu^{++} (Fig. 5A) resulted in increased TBA values. The addition of both Cu^{++} and NaCl gave results that were different with different concentrations of Cu^{++}. With 2 ppm Cu^{++}, the salt and the copper produced little or no change in the TBA values, but some seaweedy odours began to develop. When the copper concentration was further increased, salt sharply retarded the development of rancidity as indicated by TBA values and odours as compared to the controls without added salt. This retarding effect of salt on copper-induced rancidity is shown in greater detail in Fig. 6 and 7. These two sets of tests were carried out with "unsusceptible," summer-caught fish. In the first experiment, 10 different amounts of salt were added to blended muscle containing 20 ppm Cu^{++} and tested after 24, 48, and 72 hr at 0 C. In the second experiment, from 1 to 15% salt was added to muscle containing 20, 30, and 40 ppm Cu^{++} and all were tested after 24 hr. The most effective concentrations of salt for suppressing rancidity were between 1 and 8%. Three and 5% salt prevented the development of seaweedy odours and suppressed the copper-induced rancidity, even when the Cu^{++} concentration was increased to 40 ppm.

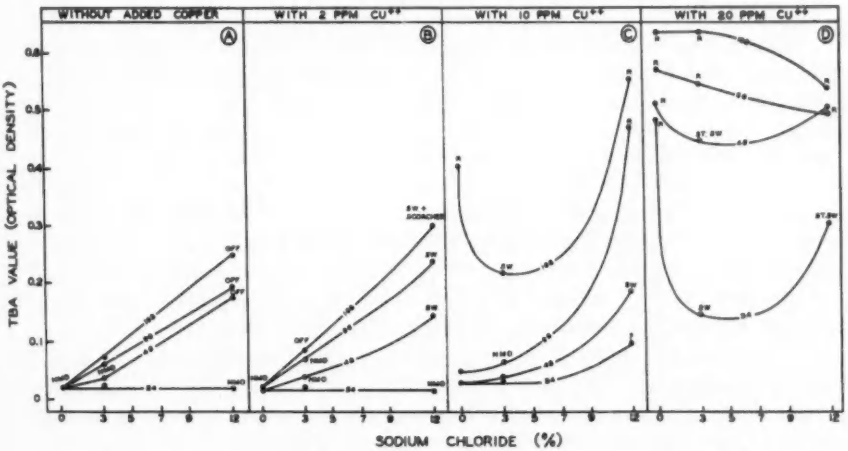

FIG. 5. Effect of sodium chloride concentration on the development of off odours and TBA values in blended muscle with 0, 2, 10, and 20 ppm added Cu^{++} and recorded after 24, 48, 96 and 168 hr at 0 C. (NMO = not much odour; SW = seaweedy; ST SW = strongly seaweedy; R = rancid; OFF = off-odour but neither seaweedy nor rancid.

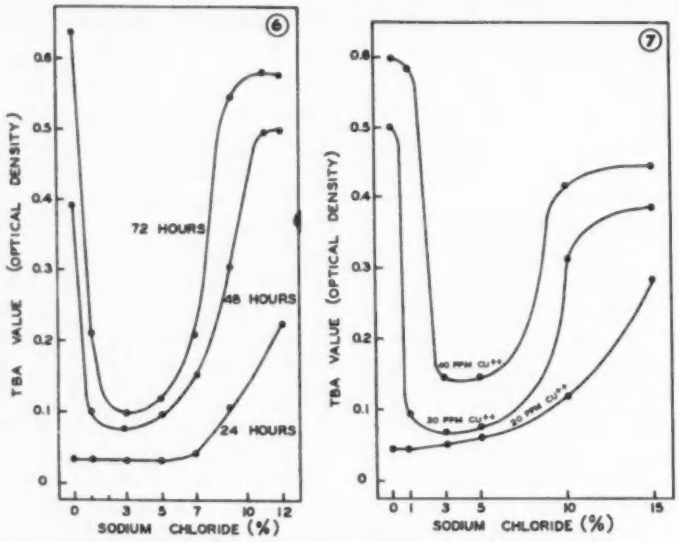

FIG. 6. The inhibiting effect of sodium chloride on Cu^{++}-induced rancidity in blended cod muscle; 20 ppm Cu^{++} was added to the muscle immediately before adding the sodium chloride. The TBA values are after 24, 48, and 72 hr at 0 C.

FIG. 7. The inhibiting effect of sodium chloride in blended cod muscle, induced by the addition of 20, 30, and 40 ppm Cu^{++}, after 24 hr at 0 C.

EFFECT OF OTHER SALTS ON RANCIDITY

Many other salts acted in a manner similar to NaCl in accelerating rancidity in the blended muscle (Fig. 8). Similar results were obtained with 13 metal chlorides (Table I). Salts in which the metals were replaced with ammonia or choline also accelerated rancidity. Addition of these salts also changed the pH of the blended muscle, which in some cases affected its physical condition by causing denaturation of the proteins, and in others causing the proteins to swell into the jellied form. Usually when the pH was below the isoelectric point of the muscle (approximately 5.0–5.3), denaturation occurred and the blend became "watery"; those with values above this level tended to form gels. As with sodium chloride, an excess of some salts caused the gel to break without necessarily lowering the pH to 5.3 or below.

Considerable variation in odours accompanied the various salt-induced rancidities. Copper and iron produced typical oily rancid odours. Strong seaweedy odours were observed with copper, iron, cobalt, cadmium, and aluminum. The other salts produced a variety of odours that were recorded as: "dried fish," "hot metal," "scallopy," "sour vegetables," "potato-like," "egg yolk," and "hydrogen sulphide." Frequently the odours were neither strong nor offensive.

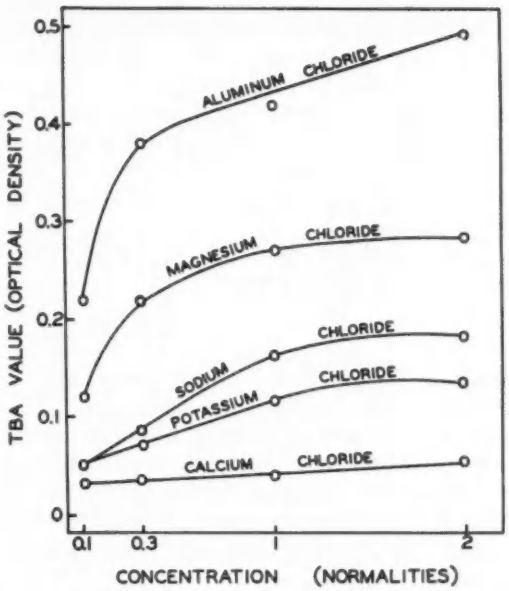

FIG. 8. Pro-oxidant effect of five metallic chlorides on the development of rancidity in blended muscle as shown by TBA values after 72 hr at 0 C.

TABLE I. Effect of normal solutions of metal chlorides on the development of rancidity in blended cod muscle held for 48 hr at 0 C.

Salt	TBA value	pH
Control	0.020	6.9
$CoCl_2.6H_2O$	0.525	5.0
$FeCl_3.6H_2O$	0.520	1.8
$AlCl_3.6H_2O$	0.460	3.4
$CdCl_2.1/2H_2O$	0.450	4.8
LiCl	0.390	6.2
$NiCl.6H_2O$	0.380	5.2
$MgCl_2.6H_2O$	0.360	5.9
$ZnCl_2$	0.330	4.8
NaCl	0.170	6.3
KCl	0.090	6.7
$CaCl_2.2H_2O$	0.030	5.5
$BaCl_2.2H_2O$	0.030	5.7

In work dealing with the effect of sodium chloride on oxidative rancidity in meats, Watts and Peng (1947) were unable to trace the effect to either sodium ions or chloride ions as such. They found that neither potassium chloride nor sodium sulphate had any effect. In the present experiments the results strongly indicate that the cations are responsible for the acceleration of rancidity, as indicated by TBA values. If the salt was also a chelating agent, such as sodium citrate or sodium oxalate, the activating effect of the cation was eliminated (Table II).

Salts other than sodium chloride also interfered with copper-induced rancidity, examples of which are shown in Fig. 9.

Antioxidants

Three commercial antioxidants ((BHT) butylated hydroxytoluene, (NDGA) nordihydroguaiaretic acid, and (PG) propyl gallate) and three chelating agents ((EDTA) ethylenediaminetetraacetic acid, sodium oxalate, and sodium citrate) were tested for their ability to retard sodium chloride-induced rancidity in fish muscle. The results, as indicated by the TBA values and odours, showed that five of these compounds strongly retarded salt-induced rancidity (Table III). The butylated hydroxytoluene had only a slight inhibiting effect.

Table II. Effect of normal solutions of different salts with similar cations on the pH of blended muscle and the development of rancidity (as indicated by TBA values) during 48 hr storage at 0 C.

Salt	TBA value	pH
Control — no salt	0.06	6.6
$MgSO_4.7H_2O$	0.35	6.1
$MgCl_2.6H_2O$	0.33	5.9
$NaNO_3$	0.29	6.8
NaCl	0.24	6.2
$Na_2SO_4.10H_2O$	0.20	6.6
KCl	0.13	6.5
K_2SO_4	0.07	6.7
$CaCl_2.2H_2O$	0.07	5.7
$CaSO_4.2H_2O$	0.06	5.9
Sodium oxalate	0.03	6.6
Sodium citrate	0.03	7.0

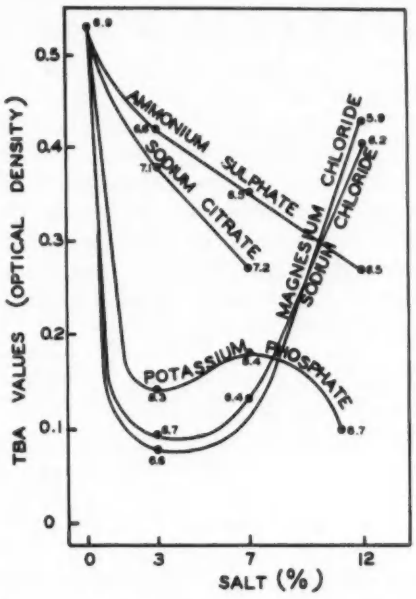

FIG. 9. The inhibition of copper-induced rancidity in blended cod muscle by the action of five different salts. TBA values measured after 24 hr at 0 C. The numbers accompanying the datum points are the corresponding pH values.

TABLE III. Effect of chelating agents and antioxidants on sodium chloride-induced rancidity in blended cod muscle after 72 hr at 0 C.

Compound added	Concentration (%)	TBA values	
		No NaCl	12% NaCl
Control	—	0.020	0.310
EDTA[a]	0.01	0.015	0.015
Sodium oxalate	10	0.020	0.035
Sodium citrate	10	0.020	0.025
BHT[b]	0.01	0.020	0.225
NDGA[c]	0.01	0.015	0.060
PG[d]	0.01	0.015	0.015

[a]EDTA — Ethylenediaminetetraacetic acid.
[b]BHT — Butylated hydroxytoluene.
[c]NDGA — Nordehydroguaiaretic acid.
[d]PG — Propyl gallate.

Effect of Impure Fishery Salts and Sea Water

It has frequently been suggested that any accelerating effect of common salt on rancidity is due to the impurities it contains rather than to the salt itself. It was shown here that reagent grade salt does catalyze rancidity. Experiments were carried out to compare the activity of pure sodium chloride with various impure "solar" and "rock" salts used in the industry. The results (Table IV) indicate that the difference between the pure and the impure salts is relatively unimportant as far as accelerating rancidity in the muscle is concerned. Sea water and 3% NaCl have also been compared for their ability to accelerate rancidity and also retard copper-induced rancidity, and both appeared to be equally effective.

Table IV. TBA values for blended cod muscle to which 10% of various fishery salts had been added and then stored for 4 days at 0 C.

Salt	TBA value
Control	0.030
Reagent grade NaCl	0.265
Turks Island solar salt	0.240
Inagua (I) solar salt	0.300
Inagua (II) solar salt	0.315
Barcelona solar salt	0.295
"Fishery" salt	0.320
African reconstituted solar salt	0.275
Malagash (impure) mined salt	0.305
Malagash (fishery) mined salt	0.315

Lipid Oxidation in Some Commercially Salted Fish

Six normal, heavily salted "green" (undried) cod and six heavily salted dried cod were obtained from a local plant. The odours were noted during, and immediately after being blended with water. The green fish were described as having a "dulse-like" odour and the older dried fish were characterized as "smelling like old rotten seaweed." The TBA values were as follows:

	Green	*Dried*
Mean TBA value	0.158	0.092
Standard deviation	0.060	0.034
Standard error	0.025	0.014

These values for the green fish are from 4 to 8 or 9 times higher than the corresponding values for fresh unsalted muscle. The values for the dried fish, which had much stronger odours, were less than those for the green fish.

Although these figures do indicate increased TBA values, they are not as high as might have been expected. Further discussion on this point must await the results of a more extensive survey which will follow the fish during various stages of salting, drying, and storage, giving results from a larger number of commercial fish and showing a greater variation in quality.

SUMMARY AND DISCUSSION

The addition of sodium chloride to blended cod muscle accelerated the development of rancidity. This salt-induced rancidity was inhibited by the chelating agents, EDTA, sodium oxalate, and sodium citrate, and by the antioxidants, NDGA and PG. Rancidity developed slowly with the addition of 1% sodium chloride; between 1 and 12% the rate increased in proportion to the concentration of salt added; further increases above 12% did not bring any further change in the rate of development.

Contrary to the findings of Watts and Peng (1947) in their study of salt-catalyzed rancidity in meat, it was found that the pro-oxidant activity of sodium chloride in fish muscle was the result of the sodium ions. Cations of other metal salts had a similar pro-oxidant effect. Using equivalent concentrations, their relative activity was in the following order: $Cu^{++} > Fe^{+++} > Co^{+++} > Cd^{++} > Li^{+} > Ni^{+++} > Mg^{++} > Zn^{++} > Na^{+} > Ca^{++} > Ba^{++}$. With a few exceptions this roughly agrees with the relative oxidizing activity of these metals as shown by their position in the electromotive series.

Although sodium chloride and many other metal salts acted as pro-oxidants when added by themselves, they had a strong inhibiting effect on Cu^{++}-induced rancidity in the fish muscle. The most effective concentrations of sodium chloride for this antioxidant effect were between 1 and 8%.

Fish muscle in which the proteins were denatured by heat or by prolonged frozen storage was much less sensitive than fresh, uncooked muscle to the rancidity catalyzed by salt.

In a previous paper (MacLean and Castell, 1964), a close correlation was found between TBA values and the development of rancid odours in fish muscle where the rancidity was induced by adding trace amounts of Cu^{++}. In this present paper it has been shown that the addition of sodium chloride to the muscle also accelerates rancidity. But there is a considerable difference between the TBA–odour relationship in the copper-induced and in the salt-induced rancidities. There was also a difference in the types of odours. This lack of a fixed relationship between TBA values and the type and intensity of accompanying odours was further emphasized by the experiments with other metal salts and with more recent, unpublished work on amino acid-induced rancidities. Pohle *et al.* (1964) have recently explored the relationship between both peroxide and TBA values and flavour scores in different formulations of lard. They came to the conclusion that the TBA value cannot be

used as an index of flavour quality unless it is part of a series on which previous data are available. This agrees completely with our observations which have been confined to odours rather than flavours. Each type of rancidity has a different TBA–odour relationship. This is very important when it comes to the interpretation of TBA values obtained from oxidized muscle from different species of fish and from the same species processed differently.

This raises the question of the origin and nature of the odours accompanying rancidity. As pointed out by Lundberg (1962), by definition the term "rancidity" is based on subjective determination of odour and flavour. But oxidative rancidity is not specific. There are many quite different odours associated with the oxidation of lipids in different fats, oils, and fatty foods. However, the term "rancidity," when applied to fish and vegetable oils that contain fatty acids with three or more double bonds, is usually associated with the familiar "oily," "fishy," and "paint-like" rancid odours that frequently develop when these materials undergo oxidation. Many of the volatile carbonyls, mainly aldehydes, responsible for these odours have been identified so that the chemical identity of rancidity in these products has been well established. With the muscle of the so-called lean fish the problem of odours associated with rancidity is much more complex. The lipids are not only present in smaller amounts, but they are chiefly phospholipids that are intimately bound up with muscle protein (Lovern, 1953). In the muscle tissue these lipids are also accompanied by many other biologically active compounds that are capable of entering into oxidation reactions. The odours accompanying lipid oxidation under these conditions may be quite different from those associated with the oxidation of the free oils alone. Kock (1962), discussing rancidity in dehydrated foods, stated that the typical autoxidation odour of lipids associated with rancidity in bulk oils and from thin films of oil spread on inert matrices was quite different from that associated with oxidation of lipids in dehydrated foods and model systems representing dehydrated foods. It was found that each dehydrated food possessed its own peculiar odour when it became oxidized. For this reason, in the early stages of the work on precooked legumes the unpleasant off-odour was not at first associated with rancidity. Something similar appears to be the case in oxidation of the lipids in the fish muscle. In addition to the characteristic oily-rancid odours that appear in the later stages, there are many other off-odours that are not usually identified with the development of rancidity; and when the rancidity is activated by different chemical compounds there is a considerable difference in these earlier off-odours.

The relationship between the ability of salt to extract proteins from the tissues and its ability to accelerate rancidity is not clear. There are, however, striking parallels in the results given by Dyer *et al.* (1950) on the effect of sodium chloride concentration on the extraction of soluble proteins from cod muscle and the observations made here on the effect of this salt in the blended muscle on the development of rancidity. Dyer *et al.* (1950) showed that there is a very rapid increase in soluble protein with increasing concentrations

between 1 and 3%. The maximum values were obtained with 3–7%, and increasing the salt beyond 12% resulted in a gradual decrease in the soluble protein in the solutions. These ranges of 1–12% and 12% to saturation correspond to the percentages of salt in the blended muscle producing jellied or watery preparations: in the former, the proteins are taking up water and swelling; in the latter, they are being denatured and giving up much of their bound water. This concentration of 12% corresponds to the point in the TBA-salt concentration curve where the addition of more salt fails to further accelerate rancidity.

It is also interesting to observe that Dyer's curve, relating the salt concentration of the extracting solutions with the degree of protein peptization, is almost the reverse of the curve showing the capacity of salt to inhibit copper-induced rancidity in the blended muscle. It seems that there might be some action of the salt on the lipoprotein cell membranes or constituents which results in one case in swelling and peptization of the protein micelles, and, in the other, in protection of the lipid from copper-induced oxidation.

As pointed out in the introduction to this paper, there is considerable evidence to indicate that with pure fats the addition of sodium chloride does not accelerate oxidation. To be effective, the salt requires the presence of enzymes, pigments, or other organic compounds. There is much to show that at least one mechanism by which salt accelerates rancidity in fish muscle is through the changes it produces in the accompanying muscle protein.

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Estimates of the Theoretical Biomass of Juvenile Winter Flounder, *Pseudopleuronectes americanus* (Walbaum) Required for a Fishery in Rhode Island[1,2]

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ABSTRACT

A model of the life history of the winter flounder was constructed using empirical estimates of vital statistics. The initial stock weight of juveniles was determined by substituting trial initial stock weight values into equations which contained average values of growth and mortality coefficients until the observed value of the equilibrium yield was approximated. Model data indicated that the stock weight of juvenile winter flounder at an age of 5 months constituted a significant proportion of the equilibrium yield even with conservative estimates of model coefficients. Growth appeared to be sufficiently rapid during early life-history stages to provide for a large increase in biomass in spite of considerable natural mortality.

INTRODUCTION

The purpose of this report is to use available data concerning the vital statistics of the winter flounder, *Pseudopleuronectes americanus* (Walbaum), to obtain preliminary theoretical estimates of the size of the population of juvenile winter flounder necessary to sustain or increase the yields of a commercial fishery for this species in a defined area (Rhode Island Sound).

Considerable renewed interest has recently been demonstrated in marine fish culture. British plaice, *Pleuronectes platessa* (Linnaeus), rearing experiments in which eggs have been incubated and larvae raised to life-history stages considerably beyond yolk-sac absorption are of special interest. Publications by Shelbourne *et al.* (1963), Shelbourne (1963a,b), and Riley and Thacker (1963) illustrate some of the recent progress. The plaice has been reared to approximately 150 days of age under controlled field and laboratory conditions. Shelbourne (1964) has recently reviewed the plaice-rearing experiments in Britain as well as other marine fish cultural activities. It has been suggested in the above-mentioned reports that the artificial propagation of marine species to later life-history stages may have direct application in the management of depleted coastal fisheries by augmenting natural recruitment.

The value of most previous marine fish cultural activities which involved liberation of larvae during or soon after yolk-sac absorption has been questionable in terms of improving yields of marine demersal fish (Shelbourne,

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1964). However, the recent developments in artificial propagation which permit rearing to later life-history stages suggest a reappraisal of the role of marine fish culture in fisheries management may be timely. This study may have some bearing on the artificial propagation of winter flounder and related species of marine fishes by indicating relationships of the biomass of juvenile fish to the yield of a fishery.

Some indication of the required magnitude and feasibility of the recently developed marine fish cultural operations can be assessed in models containing empirical life-history data for the plaice or some related species for which adequate estimates of growth, mortality, abundance, and distribution are available.

The winter flounder was considered to be suitable for this preliminary study for several reasons. 1) It is closely related to the plaice — both genera are included in the family Pleuronectidae. 2) The history of the local commercial fishery makes it possible to judge the merits of the hypothesis of an equilibrium state. 3) The winter flounder has been artificially propagated in large numbers to the stage of yolk-sac absorption (Bigelow and Schroeder, 1953). It is assumed that this species could be reared to later life-history stages in a manner analogous to the plaice. 4) The winter flounder breeds in shoal water and stocks of juvenile as well as adult fish are highly localized in spite of some seasonal movements (McCracken, 1963; Pearcy, 1962; Perlmutter, 1947; Saila, 1961). Effective management possibilities are evident for this species in view of its localization. 5) Since it has been demonstrated that breeding stocks return to former breeding grounds in shoal waters (Saila, 1961), selective breeding and elimination of undesirable stocks should also be possible. 6) The available literature for this species contains estimates of vital statistics for various life-history stages.

MODEL AND DATA

The method of Ricker (1945) for the estimation of equilibrium yield was utilized. In Ricker's model yield is equal to:

$$Y_E = \sum_{T=T_r}^{T=T_\lambda} \frac{(F_T P_{T(0)}\ (1 + e^{g_T - Z_T})}{2}.$$

Symbols for this equation follow international format to the extent possible, where:

Y_E = equilibrium yield,
T = successive intervals or periods in the life of the fish,
T_r = the first period under consideration,
T_λ = the last period under consideration,
F = the instantaneous rate of fishing mortality,
P = the weight of a group of fish,
Z = the instantaneous rate of (total) mortality,
g = the instantaneous rate of growth in weight.

A tabular computational procedure for the estimation of equilibrium yield has been described and applied by Ricker (1958). The yield equation was programmed for a digital computer (IBM 1410) because the computations were carried out over many combinations of coefficients, and the initial stock weight necessary for a known equilibrium yield was desired. The latter was accomplished by successive approximations and would have been prohibitively time-consuming by hand computations.

The major advantage of Ricker's method in this work is its extreme flexibility. For example, seasonal distributions of growth, fishing, and natural mortality could be examined. In this model growth is assumed to be logarithmic in nature over short and variable time intervals in contrast to the von Bertalanffy growth model used in the equilibrium yield equation described by Beverton and Holt (1957). Ricker's model is believed to accommodate available data for various life-history stages in a realistic fashion.

The values of the coefficients applied to the model are shown in Table I. These data were taken from Berry *et al.* (1965), and Pearcy (1962). From this table it is evident that not only were time intervals unequal but also a range of values was available for various coefficients. Table II shows that Rhode Island landings of winter flounder have been fairly stable for the past decade and averaged slightly more than 2,000,000 lb annually. The intensity of the fishery and the size of the fleet have been relatively constant over this period as adduced from knowledge of local fleet activities. The average yield was utilized as an empirical equilibrium yield from which the weight of the stock at early life-history stages was determined using estimated values for the various model parameters.

It was also clear from an examination of monthly winter flounder landings that the fishery is seasonal with highest landings during the summer months. Monthly landings were grouped into $\frac{1}{4}$-year intervals and the fishing mortality (F) values were weighted accordingly. Growth of adults was also weighted. The weighting factors for growth were the same as those observed for juveniles by Pearcy (1962). The factors used were the following:

	F	g
	Weighting factor	Weighting factor
May 1		
	.43	.375
August 1		
	.24	.375
November 1		
	.19	.125
February 1		
	.14	.125
May 1		

TABLE I. Values of winter flounder vital statistics utilized in the model.

Age	Weight	M	Range	F	Range
	g				
Birth	0.0037	0.371	0.251–0.491		
5 months	1.976	0.371	0.251–0.491		
6 months	3.351	1.113	0.753–1.473		
9 months	5.34	1.113	0.753–1.473		
1 yr	8.07	0.249	0.009–0.489		
1.25	26.53	0.249	0.009–0.489		
1.50	56.25	0.249	0.009–0.489	0.03	0.018–0.042
1.75	72.3	0.249	0.009–0.489	0.03	0.018–0.042
2.0	87.047	0.09	0.03 –0.15	0.136	0.085–0.188
2.25	115.89	0.09	0.03 –0.15	0.076	0.047–0.105
2.5	150.5	0.09	0.03 –0.15	0.060	0.037–0.083
2.75	163.42	0.09	0.03 –0.15	0.044	0.028–0.061
3.0	177.05	0.09	0.03 –0.15	0.273	0.169–0.376
3.25	211.67	0.09	0.03 –0.15	0.152	0.095–0.210
3.50	250.55	0.09	0.03 –0.15	0.120	0.075–0.166
3.75	264.5	0.09	0.03 –0.15	0.089	0.055–0.122
4.0	278.96	0.09	0.03 –0.15	0.089	0.055–0.122
12.0	873.8[a]				

Instantaneous total mortality coefficient (Z): $0.9383 < 0.9938 < 1.0524$.

[a]The table is truncated to conserve space. One quarter year values between 4.0 and 12.0 years are the same as values between 3.0 and 4.0 years.

The nature of winter flounder early life history documented by Bigelow and Schroeder (1953), Pearcy (1962), and Warfel and Merriman (1944) precludes excessive fishing mortality during early life history stages due to concentration in shallow estuaries and embayments. In the model a low value of fishing mortality was initiated (as indicated in Table I) at an age of 18 months. However, the full values of fishing mortality were applied starting at age III. This age corresponds to the approximate minimum size (10 inches) at which these fish are acceptable for processing by the local fishery. Further justification of this size limit for full exploitation is evident from the nature of the survival curve (Berry *et al.*, 1965) for Rhode Island winter flounder stocks.

PROCEDURE

The primary information of interest for our purposes was a range of values for the weight of juvenile fish necessary to sustain the existing fishery which yields approximately 2.19 million lb/year from Rhode Island waters under various combinations of mortality coefficients. The values for the biomass of winter flounder at 5 months were of particular interest because these correspond approximately to the age to which the British hatchery propagation has been attempted to date.

TABLE II. Annual trawl landings of winter flounder in Rhode Island for a 10-year period.

Year	*Landings*
	lb
1954	1,276,028
1955	1,451,521
1956	2,862,651
1957	2,685,178
1958	1,947,113
1959	2,251,646
1960	2,412,813
1961	2,027,202
1962	2,034,773
1963	2,917,455

$\bar{x} = 2{,}186{,}638$
$s = 175{,}451$
95% confidence interval for σ; $116{,}798 < \sigma < 306{,}337$

As stated previously, it was assumed that winter flounder could be reared artificially in a manner similar to the plaice-rearing experiments to an age of approximately 150 days (5 months) after hatching. The hatching date is taken as May 1 from the studies of Pearcy (1962). Pearcy also estimated the average weight of 150-day-old winter flounder at 1.976 g. This weight was considered a reasonable approximation to the weight which might be achieved in extended fish cultural operations for this species.

The procedure for estimating the weight of the stock at various life history stages involved first obtaining, by a trial procedure, values of the weight of the stock at metamorphosis (average weight of individuals at metamorphosis = 0.0037 g). Average empirical values for M, F, and g shown in Table I were substituted for all life history stages in an attempt to simulate the growth and mortality of the population. New values for the initial weight of newly

hatched larvae were substituted into the model until the model value for the equilibrium yield (Y_E) closely corresponded to the observed average sustained yield. The stock weight at metamorphosis necessary to provide an equilibrium yield of approximately 2 million lb was 6.5×10^6 g (14,300 lb). The model program also provided stock weight at all life history stages, but only the values for age 5 months will be considered further. The output from runs employing various combinations of coefficients was sufficiently voluminous to suggest a graphic portrayal of the results.

RESULTS

Figure 1 illustrates three surfaces which represent the stock weights (in grams) of winter flounder at 5 months of age required to produce an equilib-

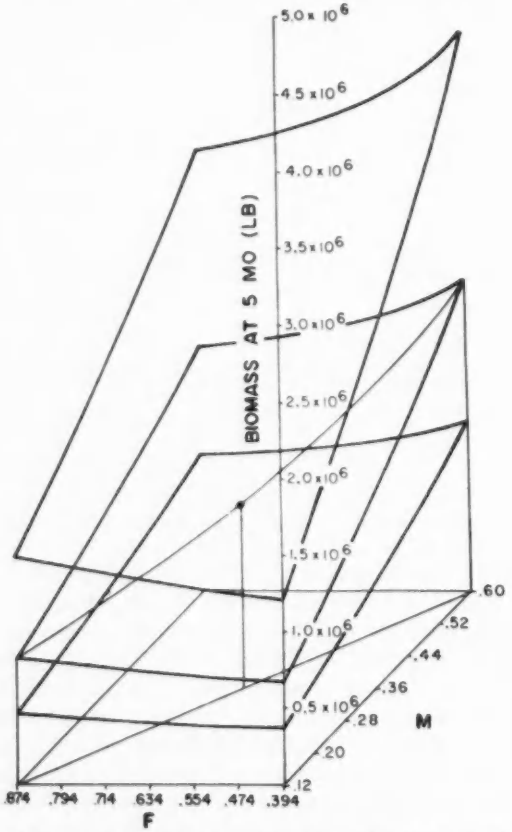

FIG. 1. Stock weights (grams) of winter flounder at age 5 months required to produce an equilibrium yield of approximately 2 million lb for three values of Z for the first 5 months. Lowest surface, Z = 1.655; middle surface, Z = 1.855; upper surface, Z = 2.055.

rium yield of approximately 2 million lb. The lowest surface represents a fairly conservative estimate of Z, the total instantaneous mortality coefficient for the first 5 months. The middle surface represents an average value, and the upper surface represents a slightly higher value. The three total instantaneous mortality coefficients for 5 months represented by the three surfaces were 1.655, 1.855, and 2.055, respectively. These surfaces include all combinations of adult natural mortality and fishing mortality coefficients combined with the three early mortality coefficients.

The middle surface is of particular interest. The estimate of total instantaneous mortality for adults (Table I) was obtained from an age frequency distribution and is considered an unbiased and realistic estimate. The vertical plane on the diagonal drawn in the base of the figure cuts the three dimensional figure at equal values of Z. The intersection of this plane with the middle surface provides estimates of the stock weight at 5 months ranging from 822,000 lb when fishing mortality is high (F = 0.874) and natural mortality is low (M = 0.12) to 2,029,000 lb with a low fishing mortality (F = 0.394) and a high natural mortality rate (M = 0.60). The point on this plane represents the best estimate of existing conditions in the fishery (F = *0.634*, M = *0.360*) to provide a stock weight at 5 months of 5.43×10^8 g or 1.2×10^6 lb.

The value of M for this study was obtained by subtracting the fishing mortality coefficient from the estimated total instantaneous mortality coefficient for Rhode Island data (0.997 – 0.637 = 0.360). An estimate of natural mortality obtained in this manner is uncertain. However, the value obtained corresponds exactly with an independent estimate made by Dickie and McCracken (1955) for a Canadian winter flounder fishery.

Data for four additional surfaces as well as the three discussed are summarized in Table III. These seven sets of data were generated from seven equal increments spanning the 95% confidence limits for the range of juvenile mortality estimates provided by Pearcy (1962). These values of biomass at 5 months range from 110,000 lb for the lowest juvenile natural mortality rate to 12,162,000 lb for the highest. It is clear that values for surfaces 5, 6, and 7 generate stock weights considerably greater than the empirical equilibrium yield of the fishery.

DISCUSSION

Several significant points are apparent from the results of these model studies.

Firstly, the stock weight of newly metamorphosed larvae necessary to sustain the empirical average yield under average observed mortality coefficients for all life-history stages was found to be 6.5×10^6 g or 1.8×10^{10} individuals. The liberation of even 10 million larvae to this highly localized fishery would add only 0.06 of 1% to the equilibrium yield if mortality and growth were similar to naturally-spawned fish. The futility of such a scheme is obvious.

Of even greater significance for the purposes at hand, is the observation that the stock weight at 5 months of age for average values of vital statistics

TABLE III. Range of biomass values at 5 months required to sustain a constant yield obtained from seven increments of age 0 and I mortality coefficients.

	Total instantaneous mortality coefficients (5-month period)		Range of biomass values
	Age 0	*Age I*	
1.	1.255	0.015	111,000– 338,000
2.	1.455	0.148	202,000– 615,000
3.	1.655	0.282	366,000– 1,115,000[a]
4.	1.855	0.415	668,000– 2,029,000[a]
5.	2.055	0.548	1,206,000– 3,651,000[a]
6.	2.255	0.682	2,033,000– 6,677,000
7.	2.455	0.815	4,041,000–12,162,000

[a]Entire surface of values plotted in Fig. 1.

consists of 1.2×10^6 lb or approximately 56% of the empirical equilibrium yield. It was shown in Table III that changes in mortality rates at early periods in the life history of the fish can be expected to cause relatively great variations in the biomass of fish available to the fishery. However, in later life-history stages the effects of mortality are proportionately less, as inferred from Fig. 1. If all of the surfaces of values expressed in Table III had been plotted in Fig. 1, the range of biomass available at 5 months of age needed to sustain the fishery would have exceeded two orders of magnitude. It is clear from these values as well as from the entire middle surface of Fig. 1 that growth is extremely rapid during early life history stages and provides for a significant early increase in biomass over and above the amount removed by natural mortality. From the middle surface in Fig. 1 it is also clear that this statement holds generally regardless of the levels of mortality (within the limits indicated) which were imposed upon the adult stock. In addition, the effect of natural mortality seems to be more significant than fishing mortality within the limits of the coefficients applied to the data. These observations tend to corroborate the equilibrium yield diagrams presented by Dickie and McCracken (1955).

Further interpretation of the range of values of juvenile mortality coefficients (up to 5 months) with various combinations of mortality coefficients for later life-history stages is desirable. The observed range of values demonstrated in Table III is great. At the lowest values of early mortality combined with the most conservative estimates of natural and fishing mortality rates a minimum stock weight of 110,000 lb at 5 months is obtained. This indicates that slightly more than 5% of the equilibrium yield is present at this time.

However, this value is believed to be low for the following reason. An estimate of the population of age I winter flounder in a defined area was made by Saila (1962). In this study an average weight of 39 lb per acre of age I winter flounder was determined. If it is assumed that this estimate represents an average standing crop then the shoal water nursery areas in Rhode Island less than 10 ft deep consisting of 16.5×10^3 acres can be multiplied by the average weight per acre to provide an empirical biomass estimate of 6.4×10^5 lb for Rhode Island waters at this age. The calculated weight at age I from model data which compares most favorably with these empirical data is 6.25×10^5 lb. It was obtained with slightly more than the average mortality coefficients described by Pearcy (1962). Two results of this comparison are suggested. Firstly, further confirmation of a high biomass estimate at 5 months is suggested. Secondly, these data suggest that the recruitment necessary to sustain the Rhode Island fishery for winter flounder may be derived entirely from the products of spawning in shallow waters. The evidence at hand indicates that extensive spawning of this population of winter flounder need not take place outside the shoal areas of estuaries.

CONCLUSIONS

It is clear from the above results and discussion that even the more conservative estimates of the stock weight of juvenile winter flounder at 150 days of age using Pearcy's (1962) average juvenile mortality coefficients indicate that a significant percentage (~ 0.30) of the equilibrium yield weight is present at 5 months. This value is obtained from the lowest corner of the middle surface of Fig. 1. If it is assumed the range of data utilized in the model study falls within the limits which actually occur in nature and that survival and growth of hatchery stock are similar to natural stocks, then the biomass of juvenile winter flounder necessary to significantly augment natural stocks is very high. It is suggested from this preliminary study that research on increasing the basic productivity of nursery areas as well as controlled pond culture would have a higher probability of success in terms of improving the fishery.

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Partial Freezing as a Means of Preserving Pacific Salmon Intended for Canning[1]

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ABSTRACT

Proteolysis of the flesh surrounding the visceral cavity ("belly-burn") can cause serious spoilage in Pacific salmon. The condition usually occurs in uneviscerated fish that were feeding when caught and develops during storage at temperatures above freezing when storage must be prolonged beyond a few days.

The possibility that the proteolysis might be prevented by partial freezing of the fish in salt-reinforced refrigerated sea water at various temperatures between 25 and 29 F was investigated. Round fish, containing large quantities of food in the stomach and intestine could be held at 25 F for 2 weeks without the appearance of belly-burn or bacterial spoilage. Between 25 and 29 F there was a delay in the appearance and a reduction in the incidence of belly-burn.

Partial freezing was effective in preventing a darkening of the flesh adjacent to the visceral cavity, a defect that is sometimes observed in fish canned after being stored in an uneviscerated condition for several days at temperatures above freezing. This darkening is apparently the result of the diffusion of pigment from the kidney, liver, and spleen into adjacent flesh.

The lipid of the red lateral muscle in partially frozen fish was found to be very susceptible to rancidity, but this defect was overcome by excluding air from the storage tank.

Free drip from partially frozen fish after storage (3.2–4.5%) was approximately double that from unfrozen fish, while weight increases during storage tended to be a little greater in unfrozen than in partially frozen fish. Spoilage odours that developed in unfrozen fish during storage were greatly reduced or eliminated in partially frozen fish. Sodium uptake and potassium loss during storage were similar in fish stored under either condition, but magnesium uptake was less in partially frozen than in unfrozen fish.

A comparison of the influence of prior storage of the fish, either unfrozen in refrigerated sea water or partially frozen in salt-fortified, refrigerated sea water on the quality of the canned product, showed that each method had some advantages over the other. When the fish were of initially good quality, those stored partially frozen yielded a product quite comparable in quality to those stored unfrozen. Judgment of quality was based on the results of a number of organoleptic and objective tests, including colour, curd formation, firmness of flesh, quantity of free oil, and odour.

INTRODUCTION

Along the coast of British Columbia salmon are commonly stored in ice or in refrigerated sea water (RSW) before being canned, and, in recent years, because of the extended storage period and the marked reduction in crushing of fish that it affords in comparison with icing, RSW has been gaining in popularity (Roach *et al.*, 1961). However, when feeding fish are taken and time does not permit evisceration before storage, severe proteolysis of the flesh

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surrounding the visceral cavity (belly-burn) can occur if storage in either ice or RSW must be prolonged beyond a few days (Barker and Idler, 1955; Ronald *et al.*, 1957). Obviously, freezing the fish could be expected to reduce or prevent proteolysis, but the fishing vessels presently engaged in the British Columbia salmon fishery are not equipped for freezing fish at sea. However, the refrigerating capacity of most of the RSW-equipped vessels is sufficient to enable partial freezing of their catch.

Although the slow freezing of fish at temperatures between 23 and 30 F and storage at temperatures between 21 and 28 F have been shown to be unfavourable from the point of view of protein denaturation (Dyer and Dingle, 1961; Love, 1962; Anderson *et al.*, 1964) and of phospholipid hydrolysis (Lovern, 1962; Lovern and Olley, 1962), a few investigators have reported satisfactory storage of fish at temperatures within this range when the period was limited to about 2 weeks. Le Danois (1920) froze fish in sea water supercooled to 25 F then stored them, glazed, at between 25 and 28 F. He reported little loss in quality during periods of 15–40 days. Hansen (1957) stored fish in seawater ice at 28–30 F, under which conditions they became partially frozen, and found them to have a little better taste and texture after periods of up to 15 days duration than fish stored in freshwater ice at about 31 F. Golovkin and Pershina (1961) reported that fish partially frozen and stored at 27–32 F for 14–15 days yielded cooked products that were "graded highly by the testing committee," although there was some reduction in the water-holding capacity of the flesh. MacCallum and Chan (1961) found the quality of fillets of cod stored in salt-fortified RSW at 30 F was maintained somewhat longer than was that of fillets of fish stored in ice or RSW at 32 F, although at 30 F partial freezing of the fish occurred. In view of these considerations and reports, it appeared worthwhile to examine the possibility that partial freezing of salmon might provide a practical means of eliminating or reducing belly-burn without being harmful to the quality of the canned product.

The present report describes the results of investigations with sockeye and coho salmon (*Oncorhynchus nerka* and *O. kisutch*) and rainbow trout (*Salmo gairdneri*). Partially frozen fish, stored between 25 and 30 F in sea water to which salt had been added to obtain the necessary lowering of the freezing point, were compared with unfrozen fish stored in RSW at 30.5 and 32 F.

MATERIALS AND METHODS

Salmon were obtained from commercial fishermen (gill net or seine net), sockeye within 1 day of being caught and coho within 2 days. Rainbow trout were held live in tanks at the laboratory and were killed as required.

In preliminary work, fish were stored in tanks with loosely fitting lids, but in most of the work reported here a cylindrical tank 6 ft in depth, equipped with a tightly fitting lid so that it could be completely filled to exclude air, was used. The temperature of the storage solution was maintained within

±0.3 F of that desired by circulating it through an external, thermostatically-controlled chiller. Artificial sea water for use as the storage solution was prepared according to Lyman and Fleming (1940) and had the following composition (grams/litre): NaCl, 23.47; Na_2SO_4, 3.92; $NaHCO_3$, 0.19; KCl, 0.66; KBr, 0.096; $MgCl_2.6H_2O$, 10.7; $CaCl_2$, 1.1; $SrCl_2$, 0.024; H_3BO_3, 0.026. The salinity of this solution was increased by addition of NaCl as required in order to obtain a freezing point just below that of the storage temperature to be used, e.g. 4% NaCl was added when the storage temperature was to be 25 F (Roach *et al.*, 1961). Sea water with NaCl added is referred to as FRSW (fortified RSW).

The occurrence and extent of belly-burn were judged by visual observation, as was reddening of flesh adjacent to the visceral cavity and the kidney. Fish were weighed before and after storage. They were suspended by the gill cover and allowed to drain in air for 1 min before each weighing.

Free drip from muscle was determined by a slight modification of the U.S. standard method for frozen cod fillets (Anon., 1961) in which the time of holding at 68 F was fixed at 2 hr for all samples. Samples for drip measurement consisted of steaks $1\frac{3}{8}$ inch thick cut from the body of the fish below the leading edge of the dorsal fin. Sodium and potassium were measured by flame spectrophotometry and magnesium by colorimetry as previously described (Tomlinson *et al.*, 1965). Oxidative rancidity was detected by odour and taste of raw or cooked muscle. Peroxide value of lipids extracted from the raw flesh was measured by the method of Tarr (1947). The peroxide value is expressed as the number of millilitres of 0.002 N sodium thiosulfate solution required in the titration of 1 g.of lipid. Fish were vacuum-packed in 0.5-lb cans and processed at 242 F for 80 min. Examination of the canned product was conducted by the Canned Fish Inspection Laboratory of the Department of Fisheries, Vancouver, B.C., particular attention being paid to color, firmness, odour, curd formation, and percentage of free oil.

Several experiments were carried out with salmon, in each of which fish stored unfrozen (at either 30.5 or 32 F) were compared with others stored partially frozen (at 25, 27.7, or 28.8 F). In one experiment with sockeye, 28 fish were used, in a second 24, while in each of four experiments with coho 24 were used. In each experiment four fish were examined and canned when the experiment was begun, and four from each temperature after storage periods of 1 and 2 weeks, and in one experiment with sockeye also after 1 day. The duration of the storage periods recorded is that from the time of commencement of the experiment, but the actual storage period was, with one exception, 1 or 2 days longer, the additional time being that which elapsed between the catching of the fish and the start of the experiment. In the single exception (Fig. 1) there was no delay between catching and the beginning of the experiment. The method and length of preliminary storage in the other experiments is indicated in the Tables.

Several experiments were also carried out with rainbow trout. In these the fish were stored in air; in sea water with or without increased salt content

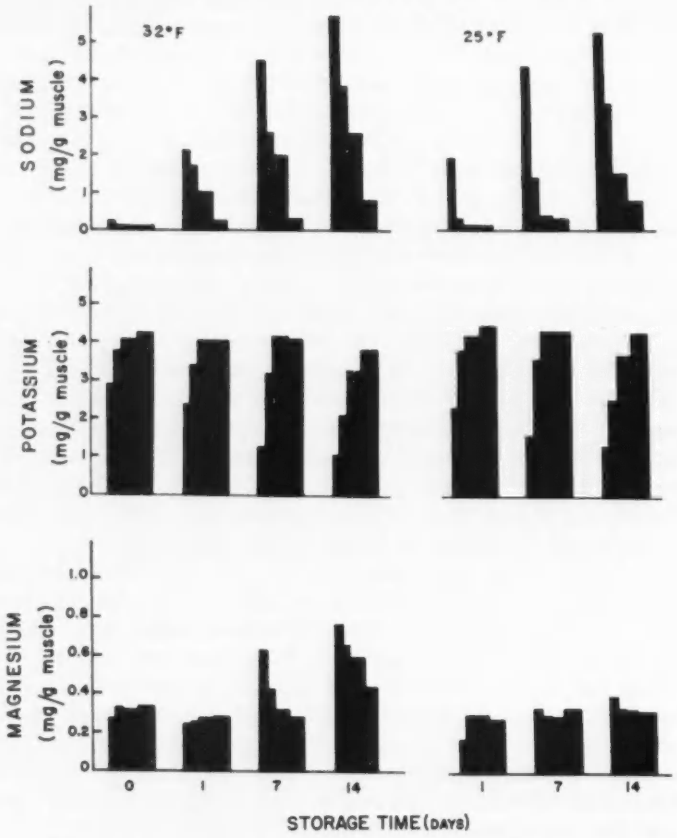

FIG. 1. Sodium and magnesium penetration into and potassium loss from sockeye salmon during storage in RSW at 32 F and in FRSW (4% added NaCl) at 25 F. In each block, the first bar at the left represents the concentration in the first $\frac{1}{8}$ inch of flesh beneath the skin, the next bar to the right that in the next $\frac{1}{8}$ inch of flesh, and the two following wider bars the concentrations in the next two $\frac{1}{4}$ inch layers of flesh in order. Each bar represents the average value for four fish.

in containers open to the air; or in the same solutions in sealed jars. The latter were sometimes flushed with nitrogen before being sealed.

RESULTS

BELLY-BURN

Belly-burn occurred irregularly and only mildly in nonfeeding sockeye stored at either 30.5 or 32 F for 2 weeks. In one experiment it was slight but noticeable at 30.5 after 1 week. At 28.8 F it was not detected at 1 week, but was noticeable after 2 weeks. At 25 F it did not occur in 2 weeks. In nonfeeding coho, slight to moderate belly-burn was observed after 2 weeks at 32 F, but not after 1 week; while at 25 F it did not occur in 2 weeks.

In light-to-heavily-feeding coho, belly-burn was negligible to moderately severe in 1 week at either 30.5 or 32 F, and slight to very severe in 2 weeks, most of the fish being in the latter condition at that time. At 27.7 F some belly-burn was found after 1 and 2 weeks in fish containing a very large amount of well-digested, unfrozen food, but none was found in other fish. At 25 F belly-burn was not detected in any fish at 2 weeks. In fish in which belly-burn was not apparent following storage, however, it appeared that the membrane lining the visceral cavity was more easily ruptured during handling than was that of freshly caught fish. The freezing point of several samples of the well-digested food from fish stored at 27.7 F was investigated and found to be about 25 F. One sample did not solidify until a temperature of 22 F was reached.

Reddening of Flesh Adjacent to the Visceral Cavity and the Kidney

At the higher storage temperatures, flesh adjacent to the visceral cavity, particularly that near the liver and kidney, became dark red in color as storage progressed, seemingly as a result of diffusion of pigment from the organs. This occurred in sockeye in 1 week at 30.5 and 32 F, in 2 weeks at 28.8 F, but not at 25 F. In coho it appeared in some fish in 1 week at 32 F and in all in 2 weeks. At 30.5 F no reddening developed in 1 week, but in 2 weeks it was slight in some fish. At 27.7 F and at 25 F no reddening occurred in 2 weeks. In sockeye held without icing at about 60 F, reddening became noticeable within 24 hr of death (experiment 1, Table III). Meyboom and van Pel (1964) have reported an apparently similar reddening in herring stored in RSW.

Weight Changes and Free Drip

Weight changes during storage were small and very variable from fish to fish. At 30.5 and 32 F the average gain in weight at the end of 1 week was 2% (range 0.2–4.6%) and at 2 weeks 3.5% (2.2–4.3%). At 25.0, 27.7, and 28.8 F the average gain was 1% (0–1.4%) at 1 week and 2.5% (0.7–6.0%) at 2 weeks, no difference between changes at the three temperatures being detected. After 1 day of storage there was a small loss in weight ($< 1\%$) by unfrozen sockeye, whereas in the partially frozen fish there was a small gain ($< 1\%$). Coho were not examined for weight changes at 1 day, since they were held in RSW about 2 days before being delivered. Consequently, the initial small losses in weight that occur when freshly-caught fish are stored in RSW would have already taken place (Tomlinson *et al.*, 1965).

The procedure followed in determination of free drip was such that the results should indicate maximum losses from this source. The fish were cut as for canning in 0.5-lb cans, and a section from near the center of the length of the fish was taken for drip measurement. The period allowed for drip to escape (2 hr at 68 F) was greater than that likely to occur in practice between cutting the fish and placing them in cans. Measured in this manner, in unfrozen fish stored at 30.5 and 32 F free drip was 2.1% (range 1.1–3.8%) at 1 week and 1.9% (0.9–3.4%) at 2 weeks, in contrast to 0.8% (0.6–1.0%) in

fish before storage. At 28.8 F drip amounted to 4% (3.4–4.5%) at 1 week and 4.5% (1.7–7.4%) at 2 weeks. At 27.7 F it was 4% (3.6–4.3%) at 1 week and 4.2% (3.4–5.8%) at 2 weeks. At 25 F it was 3.6% (2.2–5.0%) at 1 week and 3.2% (2.5–3.6%) at 2 weeks. It is clear that the average drip from the partially frozen fish was greater than that from the unfrozen fish.

Odour of Raw Fish

After 1 week of storage at 30.5 or 32 F no off-odour was detected in either the flesh or the visceral cavity of nonfeeding fish, but in heavily feeding fish, although there was no off-odour in the flesh, there was a noticeable putrid odour in the visceral cavity and gut contents of some fish. At 2 weeks there were putrid odours in the visceral cavities of both lightly and heavily fed fish, and, in some of the latter, noticeable unpleasant spoilage odour in the flesh.

At 27.7 and 28.8 F, in heavily fed fish only, there was occasional mild off-odour in the visceral cavity and gut contents at the end of 1 and 2 weeks storage, but no off-odour in the flesh. At 25 F no off-odour was detected after 1 or 2 weeks in either visceral cavity or flesh, in fact after 2 weeks at this temperature gut contents still had an odour like that of freshly killed fish.

When, in preliminary work, fish were stored partially frozen in tanks open to the air, an unusual, strong, characteristic odour developed within 1 or 2 days. This odour seemed to be related to the development of oxidative rancidity in the lipids of the red lateral muscle that also occurred under aerobic conditions, but was unlike the familiar odour of rancid fish oil. The odour has been detected in the early stages of storage of fish in RSW when the storage tank was open to the air, but under these conditions the odour disappeared as storage continued. When air was excluded from the storage tank, neither the odour nor oxidative rancidity developed in partially frozen fish of initially good quality.

Changes in Flesh Concentrations of Sodium, Potassium, and Magnesium During Storage

Changes in muscle concentrations of sodium, potassium, and magnesium that took place in the outer $\frac{3}{4}$ inch of the dorsal muscle of sockeye salmon stored either at 32 F in RSW or at 25 F in FRSW are presented in Fig. 1. After 2 weeks at either temperature, sodium, in the first $\frac{1}{8}$ inch of muscle beneath the skin, reached a concentration a little higher than that commonly accepted as most palatable (equivalent to 1% NaCl). In the next $\frac{1}{8}$ inch the concentration was a little lower and in the next $\frac{1}{2}$ inch was much lower. As a result the average value in the muscle was such that after 2 weeks the sodium concentration was a little below the most palatable concentration at these and at the other temperatures investigated, although it exceeded that concentration in some fish (Table I). The increase in sodium concentration was a little greater in the partially frozen fish than it was in those stored at

TABLE I. Sodium and potassium in the flesh of salmon after storage in RSW or FRSW at various temperatures.[a]

Experiment No.	Temperature F	Days stored			Days stored		
		0	7	14	0	7	14
		Sodium (mg/g muscle)			*Potassium (mg/g muscle)*		
1	30.5	0.30 (0.25–0.40)	2.21 (2.01–2.58)	3.17 (2.18–4.18)	3.90 (3.57–4.25)	2.42 (2.24–2.72)	1.97 (1.63–2.45)
	28.8		2.60 (1.70–3.06)	3.77 (2.92–5.85)		2.58 (2.08–3.10)	2.35 (1.84–2.68)
2	30.5	0.28 (0.23–0.38)	2.24 (1.36–3.02)	2.80 (2.58–3.27)	4.08 (3.74–4.39)	2.88 (2.42–3.20)	2.34 (2.11–2.74)
	27.7		1.74 (0.85–2.72)	3.64 (2.72–4.42)		3.17 (2.86–3.50)	2.50 (2.01–2.75)
3	30.5	0.62 (0.41–0.71)	1.51 (1.09–2.82)	3.17 (2.89–3.57)	3.57 (3.36–3.78)	3.30 (2.89–5.24)	2.35 (1.97–2.62)
	25.0		1.91 (1.33–2.78)	3.66 (3.81–4.22)		3.11 (2.89–3.40)	2.61 (2.14–2.96)

[a]Sodium and potassium measured in a sample like that taken for drip determinations, but with skin and bones removed. Fish not frozen at 30.5 F but partially frozen at the other temperatures. FRSW used at lower temperatures. Sockeye in experiment No. 1, coho in 2 and 3. Preliminary storage: experiment No. 1, 1 day, not iced; No. 2, 1 day, iced; No. 3, 2 days, RSW. Values given are averages for four fish. The range is indicated in parentheses.

30.5 F after 2 weeks, but at 25 F it was a little lower than at 32 F (Fig. 1). It thus appears that the lowering of the storage temperature largely overcomes the effect of the accompanying necessary increase in the sodium concentration of the storage solution insofar as sodium penetration into the fish is concerned. A similar observation has been reported by MacCallum and Chan (1961). Examination of Fig. 1 and Table I will show that losses of potassium were a little smaller from the partially frozen than from the unfrozen fish. Changes in magnesium concentration were small (Fig. 1) in comparison with those of sodium and potassium. These changes were much smaller at 25 F than at 32 F, but were of sufficient magnitude to be of possible significance in retarding development of toughness (Buttkus and Tarr, 1962).

Occurrence of Oxidative Rancidity Under Aerobic Storage Conditions

In preliminary experiments, when either sockeye or coho salmon, canned after storage for 1 or 2 weeks at 25 F in tanks open to air, were examined within 1 month of being canned, distinctly rancid odour and flavour were found, particularly in the red lateral muscle. The defect was most pronounced in fish canned after 2 weeks storage. When other samples from the same fish were examined 3 months after being canned, the rancid odour and flavour were not detected in fish canned after 1 week of storage, but were very strong in those canned after 2 weeks. In fish canned after storage for 2 weeks in RSW at 32 F under similar aerobic conditions, slight rancidity was occasionally detected in the red lateral muscle.

An experiment with rainbow trout, in which the peroxide value of lipid extracted from the red lateral muscle was determined, confirmed the very rapid development of rancidity in partially frozen fish stored in FRSW under aerobic conditions (Table II). Comparable rapid development of rancidity

Table II. Peroxide value of lipid from the red lateral muscle of rainbow trout stored under various conditions for periods up to 14 days.

Fish stored in	Temperature	Peroxide value[a] after		
		4 days	7 days	14 days
	F			
RSW[b]	32	3.9	2.5	6.7
FRSW[b] (4% added NaCl)	25	5.2	8.8	22.3
Air	32	3.2	2.1	2.5
Air	25	3.1	2.7	2.1
Ice	32	2.3	2.2	4.1

[a]The peroxide value for lipid from a freshly killed fish was 1.6.
[b]In tanks open to air.

did not occur under the other storage conditions examined. However, slight rancidity did appear in fish stored 2 weeks at 32 F in RSW or in ice, although none was detected in fish stored in air at either 25 or 32 F. Further experiments were conducted in which the development of rancidity in trout stored at 25 F in open tanks was compared with that in fish stored in sealed jars. Under both conditions the storage solution was FRSW (4% added NaCl), and the fish to solution ratio was 4:1 (weight:volume). Some of the jars were flushed with nitrogen gas for 2 hr before being sealed, some were completely filled with solution and sealed, while others were left with a 10% air space and sealed. Rancidity developed noticeably in fish in open tanks in 3 days, strongly in 6, and very strongly in 9. In sealed jars with 10% air, rancidity was not detected at 3 days, but was noticeable after 6 days. In filled jars and in jars flushed with nitrogen gas, rancidity was not detected after periods up to 14 days. In subsequent work with salmon, storage tanks were filled with solution and sealed during the storage period and no further trouble with development of rancidity was experienced in fish of initially good quality.

Canned Product

Data from three representative experiments are presented in Table III. The first of these was carried out with sockeye salmon of good initial quality, the other two with late-run coho salmon of variable and rather poor initial quality. The late-run coho were in an advanced stage of sexual development, and the color and condition of their flesh (particularly of the fish of experiment 3, which were later run than those of experiment 2) were extremely variable when they were caught.

It will be seen that there was little to choose between fish canned after being stored partially frozen and those stored unfrozen, such differences as occurred usually but not always tending to favour the partially frozen fish.

Darkening of flesh adjacent to the visceral cavity was delayed or eliminated in the partially frozen fish, and these fish did not soften during storage as did the unfrozen fish. The degree of darkening in fish stored in RSW was somewhat variable from experiment to experiment. The data of experiment 1 show a delay in development of darkening at 28.8 F, but in experiments 2 and 3 little darkening was observed in any of the fish. However, in two other experiments with coho very noticeable darkening occurred in RSW (32 F), whereas none was observed at 25 F.

Storage by either procedure had some effect on the flavour and odour of the subsequently canned product. With fish of good initial quality, these changes seemed to involve some loss of the initial sweet, fresh flavour rather than a development of new flavour or off-odour (experiment 1), but in fish of inferior initial quality there was a tendency for some deterioration of odour to occur (experiment 3). In experiment 3, the small but clear increase in non-specific spoilage odour that occurred in RSW-stored fish was not nearly as marked as would have been expected from the odour of the raw flesh of these

TABLE III. Comparison of salmon canned following storage in a partially frozen condition in FRSW with that canned following normal RSW storage.

Precanning storage	Colour of flesh	Curd	Darkening of flesh next to visceral cavity	Firmness of flesh	Odour		Free oil
					R	N	
Experiment 1							
Not iced (1 day)	4.8	20	0.45	9.6	0	0	2.9
RSW 30.5 F							
1 week	4.8	30	1.15	9.3	0	0	1.1
2 weeks	5.8	5	2.10	10.5	0	0	1.3
FRSW 28.8 F							
1 week	4.8	30	0.50	9.6	0	0	1.5
2 weeks	5.2	5	1.85	9.2	0	0.15	1.6
Experiment 2							
Iced (1 day)	4.0	5	0	9.6	0.12	0	4.4
RSW 30.5 F							
1 week	5.3	0	0	9.9	0	0	0.6
2 weeks	4.1	0	0.17	11.9	0.33	0.20	0.8
FRSW 27.7 F							
1 week	5.7	5	0	9.5	0.25	0	0.7
2 weeks	3.5	35	0	9.3	0.20	0.15	0.9
Experiment 3							
RSW (2 days)	3.5	0	0.05	10.6	0.45	0.15	1.3
RSW 30.5 F							
1 week	4.5	5	0	9.5	0.30	0.30	0.9
2 weeks	4.9	5	0.15	12.5	0.55	0.70	0.8
FRSW 25 F							
1 week	2.4[a]	15	0	9.2	1.00	0.20	0.7
2 weeks	3.6	0	0.25	9.7	0.60	0.25	0.9

The values are averages for 20 cans made up of four sets of five cans, each set from a different fish. Explanation of the recorded values:

Colour: 1–3, below average; 4, average; 5–7, above average.

Curd: Percentage of cans showing presence of curd in "buttons" with a diameter in excess of $\frac{3}{4}$ inch.

Darkening of flesh next to visceral cavity: On a scale ranging from 1 (slight darkening) to 3 (very pronounced darkening).

Firmness: Penetrometer reading in milimetres as determined with an instrument measuring the penetration of 12 interlocked needles pressed downwards by means of a 1-lb weight for 5 sec. The body of each needle was 1.4 mm in diameter, the tip, 0.4 mm. A value of 11 indicates slightly soft, 12 and above, soft.

Odour: R, rancidity; N, nonspecific spoilage odour, on a scale ranging from 0 (good) to 8 (very offensive). The maximum R value observed in an individual can was 3 (in one can only), the maximum N value was 2. The maximum average R value per can for five cans from a single fish was 1.2 and the maximum average N value was also 1.2. A value of 1 indicates "slight trace" and 2 is "slightly suggestive of spoilage."

Free oil: The volume of the free oil found in the can expressed as percentage of the weight of the can contents.

[a]All cans from one fish in this group had a colour rating of 1.

fish prior to canning which was bad in comparison with fish stored at 25 F. Odours present in the raw flesh were obviously diminished during canning.

Although the data for individual experiments provided no consistent evidence for a serious influence by either method of storage on the colour of the flesh or on the quantity of curd formed during canning, there appeared to be a tendency for RSW-stored fish to have a little better colour than the FRSW-stored fish and for the latter, overall, to have a little more curd ($12\frac{1}{2}\%$ of the cans of RSW fish showing curd in comparison to 15% of the FRSW fish). There also appeared to be an overall tendency to an increase in curd as a result of storage by either method, $8\frac{1}{3}\%$ of the control cans showing curd in comparison with a combined average of $13\frac{3}{4}\%$ for the cans from stored fish. Schmidt and Idler (1958) earlier reported that the colour of canned sockeye was not adversely affected by storage of the raw fish in RSW (30 F), but these investigators (1955) did observe an increase in curd in both coho and sockeye salmon during storage in RSW.

During storage by either procedure, there was a distinct decrease in the quantity of free oil found in the subsequently canned product. The decrease, which seemed to occur during the first week of storage, was unexpected and the reason for it is not known. This matter requires further investigation. C. T. Carlson of the Bureau of Commercial Fisheries, Gloucester, Mass. (personal communication) has reported finding only about one-tenth as much free oil in alewife (*Pomolobus pseudoharengus*) canned after 9 months storage at −5 to −10 F as in alewife canned fresh.

DISCUSSION

It is significant that the darkening of flesh adjacent to the visceral cavity in the canned fish closely paralleled the reddening of raw flesh in the same region. Apparently these defects are caused by diffusion of heme pigment from organs such as kidney, liver, and spleen into nearby flesh during storage. When the fish are processed, the diffused heme pigment changes color from red to brown (Tappel, 1964). Partial freezing, depending on the degree, can delay or eliminate these undesirable changes by delaying or preventing the diffusion.

Although drip losses were greater from partially frozen fish than from those stored unfrozen, as expected, it is probable that if severe belly-burn occurred in the unfrozen fish the loss from that cause would far exceed the possible loss resulting from increased drip in the partially frozen fish. The smaller quantity of drip from fish following storage at 25 F in comparison with that from fish stored at 27.7 or 28.5 F probably reflects a smaller degree of protein denaturation at the lower temperature (Love, 1962; Love and Elerian, 1964). In this connection Love has suggested that if fish are to be stored at temperatures near their freezing point, it would be preferable to keep the temperature below −3 C (26.6 F) in order to minimize protein denaturation.

The rapid development of rancidity in partially frozen fish stored in FRSW under aerobic conditions cannot in the present instance be attributed to an effect of the increased salt content of the muscle alone (Stansby and Harrison, 1942; Tarr, 1944), since salt penetration into the flesh was about the same at all temperatures of storage in sea water. In addition, Peters *et al.* (1964b) have reported that development of rancidity in whiting and pollock stored in RSW was related to oxygen availability, and that the rate was not accelerated by the presence of sodium chloride. It seems likely that development of rancidity in the present work was a consequence of a reduction or cessation of bacterial growth at the partial freezing temperatures (Shewan, 1961; Michener and Elliott, 1964; Hansen, 1963) since it is known that reducing systems of bacteria inhibit peroxide formation (Tarr, 1944). However, Peters *et al.* (1964a) found that rancidity developed in winter-caught whiting and pollock stored in RSW in the presence of either high (7 million/ml) or low (40,000/ml) bacterial counts in the water. Absence of rancidification in fish stored in air at 25 F probably resulted from the glazing of fish that occurred under these conditions (Tarr, 1944).

A strong, characteristic odour in the partially frozen fish, and of a relatively weak odour in the unfrozen fish in the early stages of storage under aerobic conditions only, suggests an explanation for the unfavourable report by MacCallum and Chan (1961). In their work, regarding the odour and flavour of RSW-stored cod, the fish were stored under aerobic conditions. The development of rancidity in RSW-stored cod observed by MacCallum and Chan (1961) and in herring by Gakichko *et al.* (1962) and Konopkaite *et al.* (1962), may have arisen from the same cause. In this connection, Meyboom and van Pel (1964) found that in canned herring the oil of fish previously stored in ice was rancid, whereas oil of fish stored in de-aerated RSW was not. However, other factors in addition to aeration (e.g. bacterial growth) are probably involved, for Reay (1958) has reported investigations into the storage of cod in deliberately aerated RSW in which apparently no untoward off-odours or rancidity were encountered. Under operating conditions at sea, the complete filling of storage tanks with sea water necessary to maintain stability of the vessel (Roach *et al.*, 1961) should eliminate difficulties resulting from aeration.

In conclusion, it appears that partial freezing of salmon in the manner described, while not ideal, provides a practical means of reducing losses from belly-burn, from darkening of flesh adjacent to the visceral cavity, and from bacterial spoilage for periods of up to 2 weeks if evisceration and rapid processing of the fish after catching are impossible. It should be emphasized that fish must be of good quality when first stored if satisfactory results are to be obtained.

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Distribution of Certain Crustaceans and Fishes in the Region of Algonquin Park, Ontario[1,2]

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ABSTRACT

Senecella calanoides, *Limnocalanus macrurus*, *Mysis relicta*, *Pontoporeia affinis*, and *Myoxocephalus quadricornis* were found in 63 lakes in the Algonquin Park region of Ontario. Their distribution results from direct coverage by glacial Lake Algonquin, outlet channels from this lake and Nipissing Great Lakes to the Ottawa valley, and inundation by the Champlain Sea. Their occurrence in 12 high-altitude lakes resulted from their transport to these waters by proglacial lakes.

INTRODUCTION

Research on glacial relicts has been carried out in Europe and Asia for over 100 years. Segerstråle (1957, 1962) has reviewed the history of relict investigations in these areas. Few studies have been made of North American relict fauna and distributional data are quite limited. Ricker (1959), who has carried out the most comprehensive survey for this continent, lists some 48 lakes in which the malacostracans *Mysis relicta* and *Pontoporeia affinis* are known to occur. These lakes are larger bodies of water and generally in basins formerly occupied by Pleistocene glacial lakes. The presence of relict species in 63 small inland lakes in Ontario ranging up to altitudes of 1250 ft above sea level is therefore a matter of interest.

The area of the present survey is shown in Fig. 1 and 2. The region included lies between Georgian Bay (Lake Huron) and the Ottawa River and is centered around Algonquin Provincial Park. The following relict species were found in the survey area: the copepods *Senecella calanoides* and *Limnocalanus macrurus;* the malacostracans *Mysis relicta* and *Pontoporeia affinis;* and the sculpin *Myoxocephalus quadricornis*.[3]

GLACIAL HISTORY

As the present-day distribution of the relict forms is to be related to the glacial history of the area, a review of events in the late Pleistocene is first necessary.

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[3]Nomenclature of fishes: Special Publication No. 2, American Fisheries Society, 1960.

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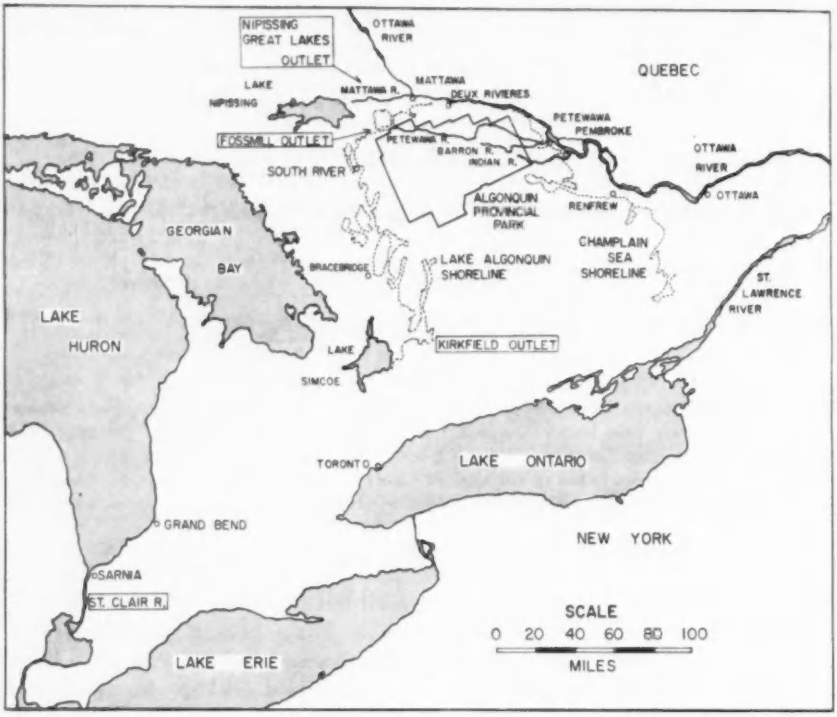

FIG. 1. Part of the Province of Ontario showing study area and glacial and marine waters of the late Pleistocene.

During the retreat of the Wisconsin Glacier the earth's surface was depressed. Salt water submerged the St. Lawrence lowland and Ottawa valley while in the basin of Lake Huron glacial Lake Algonquin covered much of the area east of Georgian Bay.

In the Georgian Bay–Ottawa valley region there are no known moraines extending continuously across the area to mark the ice-front at any stage. However, there are small discontinuous moraines running east and west. Striae on the bedrock point to the south or a few degrees west of south, supporting the concept of a general east–west trend of the ice front during the recession of the glacier.

In the Lake Huron basin glacial Lake Algonquin owed its existence to isostatic depression of the earth's crust north of Grand Bend. The amount of depression increased northward. Eventual resurgence of this land raised the shoreline of the ancient lake differentially so that it now occurs at 605 ft at Grand Bend and Sarnia, 853 ft at Kirkfield, and 1220 ft at South River (Goldthwaite, 1910). The first outlet was out the St. Clair River southward as at present. Later an outlet eastward was uncovered at Kirkfield towards Lake

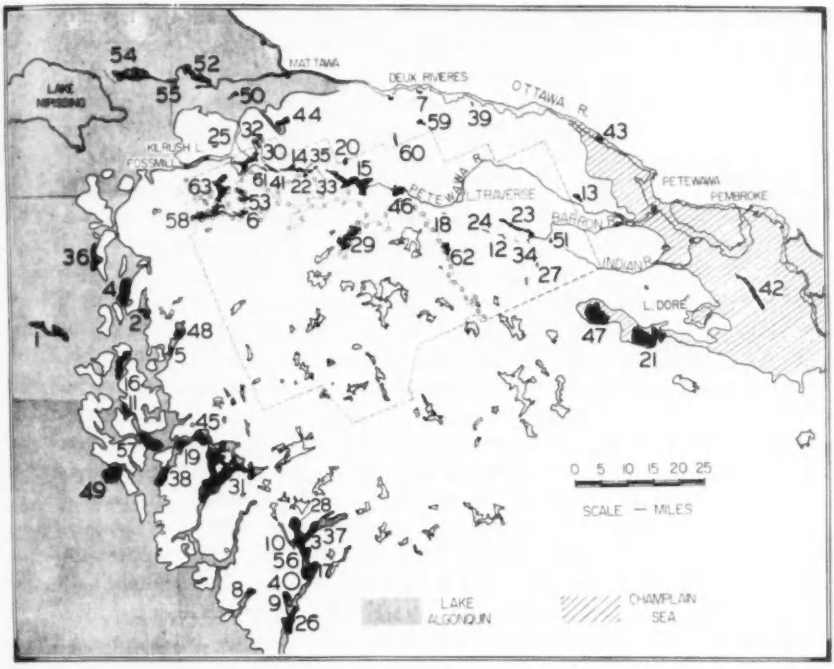

FIG. 2. Distribution of relict species. Solid lakes contain one or more relict species, open lakes are deeper lakes where they are absent. Line of circles represents 1250-ft contour. Numbers refer to lakes in Table I.

Ontario. North of Kirkfield no other outlet channel occurs eastward until Fossmill is reached (Chapman, 1954). This has been confirmed in the last 3 years by a thorough survey of the slope south of Fossmill. The highest Algonquin shoreline is mapped in Fig. 1 and 2. Although the beach is not well developed, lacustrine sediments are found generally in depressions below this shoreline.

Varved clay and sandy sediments extend to Fossmill. Immediately north of that point they are not found above the level of the outlet. The sill is 6 miles east of Fossmill at the east end of Kilrush Lake where there is a gravel terrace on which stands Canada Bench Mark Number 2487 at 1130 ft above sea level.

This outlet channel extends down the Petawawa River through a series of lakes and connecting valleys. Where the valley is narrow the bedrock of the valley sides are well scoured and where the gradient is rapid the valley floor is often paved with large rounded boulders. Broader, more level sections of the valley are usually covered with gravel and sand deposits. Below Lake Traverse the main channel followed the Petawawa River and leads to the extensive deposits of delta sands in the Petawawa area. The Barron River, and to a lesser extent the Indian River, provided alternate distributaries which con-

tributed to the building of the Petawawa delta. This sand plain stands at a maximum elevation of about 550 ft above sea level which represents the level of the Champlain Sea in that area.

As shown on Fig. 2 the Fossmill channel passes through Kioshkokwi (30), Mink (41), Cauchon (14), Little Cauchon (35), Laurie (33), Cedar (15), Radiant (46), and Traverse Lakes. The alternate route towards the Barron and Indian Rivers passes through Grand (23) and St. Andrews (51) Lakes. Side channels pass through Whitebirch Lake (61), through Eustache Lake (18), and through Greenleaf (24), Carcajou (12), and Little Carcajou (34) Lakes.

North of Fossmill the varved clays and sandy sediments of Lake Algonquin skirt the high lands and extend eastward to the vicinity of Mattawa where they terminate. A search for outlet channels running eastward across the slope southeast of Mattawa has failed to find them. There certainly is none at Deux Rivieres where a large esker running south is not cut through at any point in its course upslope between 600 and 1000 ft above sea level. Another esker contacted 4 miles southeast of Mattawa shows no gaps above 875 ft that may have been cut by a stream of water running across this rocky slope. Below 875 ft the esker loses its form making the identification of a spillway indefinite.

The Mattawa and Ottawa Rivers served at a later period as the outlet for the Nipissing Great Lakes. In the Ottawa valley the approximate limit of submergence is shown in Fig. 1 and 2. Marine shells have been found as far up the valley as Pembroke (Terasmae and Hughes, 1960). Golden Lake (21), Round Lake (47), and Muskrat Lake (42) are all within the Champlain Sea borders.

RELICT DISTRIBUTION

As Fig. 2 indicates there is, with a few notable exceptions, a clearcut relationship between these specific geological events and the present-day distribution of the relict forms in the Algonquin Park area. They occur (a) in the area previously covered by Lake Algonquin, (b) along the Fossmill and Nipissing Great Lakes outlet channels, and (c) in the area inundated by the Champlain Sea. This relationship between glacial waters and relict distribution is particularly evident along the lower Lake Algonquin shoreline. Here, immediately neighbouring lakes may be positive or negative for relicts dependent on which side of the old shoreline they occur.

The remaining 12 higher-level lakes which contain one or more relict species were never directly connected with any of these waters. The most likely explanation for these occurrences is that readvances of the glacier were attended by proglacial lakes in which the organisms could have been carried upslope from the Fossmill channel to Waskigomog (58), Wilkes (63), Biggar (6), Threemile (53), Gouinlock (22), Hogan (29), White Partridge (62), and Guthrie (27) Lakes. Similarly a later readvance from the Mattawa area could have carried the relicts upslope from the Mattawa and Ottawa valleys (Nipissing Great Lakes outlet) to Guillmette (25), Gilmour (20), Wendigo (60), and Waterloo (59) Lakes.

This concept of proglacial lakes as a mechanism in the dispersal of living organisms is widely accepted. Segerstråle (1962) and Ricker (1959) believe it adequately explains the distribution of glacial relicts in continental North America. In the present survey the absence of relict species in the area west and south of Algonquin Park above the level of Lake Algonquin supports this theory. Here any readvance of the ice would be downslope and not from water on to land as in the north and east and so the relicts could not be picked up. The fact the relicts occur up to but not over 1250 ft above sea level and many or all occur in individual lakes also signifies a major dispersal mechanism.

The troutperch (*Percopsis omiscomaycus*) and the shortjaw cisco (*Coregonus zenithicus*) have distribution patterns similar to those of the relict forms. Although sampling for these species was restricted to Algonquin Park proper both fish were found only in lakes occupied by the relict species, or, as in the case of *Percopsis*, shallow lakes directly connected to such waters. The troutperch was found in 12 of the relict lakes and five shallow adjoining lakes. The cisco was identified from six of the lakes containing relict species. It is possible these two fishes arrived in the Algonquin Park area in the same manner as did the relict forms.

ECOLOGICAL OBSERVATIONS

As indicated in Table I, the relicts may inhabit quite small lakes. They were found in 52-acre Little Carcajou Lake (34) and a number of lakes between 100 and 500 acres. None, except for the occurrence of *Senecella calanoides* in Cartier Lake (13), was found in lakes less than 80 ft deep. A number of lakes of maximum depths of 70–80 ft in areas known to have been previously covered by glacial waters was found to be negative for relict species. *Limnocalanus macrurus* and *Pontoporeia affinis* were generally found in deeper lakes than *Senecella calanoides* and *Mysis relicta*. *Mysis* appears to be the most widespread of the relict species occurring in 57 of the 63 relict-positive lakes in the present survey.

Myoxocephalus quadricornis was only taken in Cedar Lake (15). As this species is somewhat difficult to catch it may however occur in other lakes. One specimen 10 mm long (standard length) was captured in a bottom tow in mid July in 60–90 ft of water. Scott (1961) has presented some notes on the Algonquin Park collections of *Coregonus zenithicus* from White Partridge Lake (62). These are dwarf forms maturing in their second year of life at a length of 82–85 mm (standard length). They were approaching spawning condition by mid October. This species was generally caught in over 70 ft of water.

Mysis relicta, *Pontoporeia affinis*, and *Coregonus zenithicus* are all important elements in the diet of the lake trout (*Salvelinus namaycush*) in the lakes in which they occur. Parasitological studies carried out by Drs R. S. Freeman and R. C. Anderson of the Ontario Research Foundation indicate a relationship between certain fish parasites and one of the relict species (R. S. Freeman, personal communication). The bladder worm (*Cystidicola* sp.) of trout and whitefish (*Coregonus clupeaformis*) has only been found in lakes containing

TABLE I. Relict fauna distribution. Numbers locate lakes in Fig. 2.

No.	Water	Area (*acres*)	Altitude (*ft*)	Depth[a] (*ft*)	Relict species[b]			
					Senecella calanoides	*Limnocalanus macrurus*	*Mysis relicta*	*Pontoporeia affinis*
1	Ahmic	4,500	917	90+	+	+	+	...
2	Armour	1,320	1,050	166	...	+	+	...
3	Beach	1,332	1,013	108	+	...	...	+
4	Bernard	5,184	1,082	152	...	...	+	...
5	Bethune	277	1,100	81	+	...	+	...
6	Biggar	916	1,222	103	+	–[c]	+	+
7	Big Gibson	120	...	126	...	...	+	...
8	Big Trout	475	1,010	86	...	...	+	...
9	Bob	525	924	110+	...	...	+	+
10	Boshkung	1,726	1,013	178	+	+	+	+
11	Buck	526	...	92	...	...	+	+
12	Carcajou	205	829	142	+	+	+	...
13	Cartier	650	...	70	+	...	...	...
14	Cauchon	877	1,066	142	...	...	+	+
15	Cedar	6,400	1,007	195	+	–	+	+
16	Doe	2,256	956	93	+	+	+	...
17	Elsie	704	1,002	81	+	+	–	+
18	Eustache	98	...	300	+	...	+	+
19	Fairy	1,668	931	228	+	...	+	...
20	Gilmour	404	1,022	82	–	–	+	+
21	Golden	8,828	556	84	+	–	+	–
22	Gouinlock	172	1,125	854	...	...	+	+
23	Grand	1,792	730	128	+	+	+	–
24	Greenleaf	153	819	235	+	+	+	+
25	Guillmette	150	1,100	110+	+	...	+	...
26	Gullfoot	2,490	885	140	+	+	+	...
27	Guthrie	111	895	110+	+	+	+	+
28	Halls	1,368	1,069	174	...	+	...	...
29	Hogan	3,072	1,250	96	+	...	+	–
30	Kioshkokwi	2,560	993	130	+	–	+	+
31	Lake of Bays	15,260	1,034	240	...	...	+	+
32	Lauder	499	1,043	115	+	+	+	–
33	Laurie	158	1,026	93	+	...	+	+
34	Little Carcajou	52	780	160+	+	+	...	+
35	Little Cauchon	646	1,066	153	+	...	+	+
36	Machar	2,252	1,166	80	+	...	...	...
37	Maple	824	1,032	102+	+	...	+	+
38	Mary	2,000	921	163	+	...	+	+
39	McSourley	70	...	110	...	...	+	+
40	Minden	772	1,003	100	+	+	+	+
41	Mink	555	1,034	144	+	+	+	+
42	Muskrat	2,924	404	198	–	+	+	+
43	Ottawa R.	...	...	...	+	+	+	...
44	Papineau	574	995	80	...	...	+	...
45	Peninsula	1,625	931	115	+	...	+	...

(*Continued*)

TABLE I. Relict fauna distribution. Numbers locate lakes in Fig. 2. — (*Concluded*)

No.	Water	Area (*acres*)	Altitude (*ft*)	Depth[a] (*ft*)	Relict species[b]			
					Senecella calanoides	*Limnocalanus macrurus*	*Mysis relicta*	*Pontoporeia affinis*
46	Radiant	1,568	914	110+	+	...	+	...
47	Round	7,360	560	180	+	–	+	+
48	Sand	1,396	1,110	125	+	...	+	+
49	Skeleton	4,845	920	213	...	...	+	+
50	Smith	457	...	94	+	+	+	...
51	St. Andrews	222	730	80	+	+	+	...
52	Talon	3,488	636	192	+	+	+	+
53	Threemile	1,004	1,250	120	...	...	+	+
54	Trout	4,624	663	215	+	...	+	+
55	Turtle	524	663	168+	+	+	+	+
56	Twelve Mile	860	1,009	85+	+	+	+	+
57	Vernon	3,810	931	137	+	...	+	...
58	Waskigomog	3,328	1,215	106	+	...	+	+
59	Waterloo	444	907	92	...	...	+	+
60	Wendigo	401	1,040	95	+	...	+	...
61	Whitebirch	204	1,080	92	...	...	+	...
62	White Partridge	1,408	1,155	147	+	–	+	+
63	Wilkes	3,584	1,129	106	+	...	+	+

[a]Plus sign indicates lake at least this depth.
[b]*Myoxocephalus quadricornis* only taken in Cedar Lake.
[c]Known to be absent.

relicts and the role of one of these possibly either *Mysis* or *Pontoporeia* as an intermediate host seems likely. In addition the tapeworm *Cyathocephalus* sp., known to have *Pontoporeia* as an intermediate host, was also found.

DISCUSSION AND CONCLUSIONS

This survey extended the known North American distribution of relict fauna. The origin of the relicts in the Algonquin Park region of Ontario appears to be from two primary sources, glacial lakes and rivers and marine submergence. In the former case a secondary distribution is attributed to higher altitudes by proglacial lakes.

The survey was reasonably complete in the area from the Lake Algonquin shoreline across Algonquin Park to the Mattawa and Ottawa Rivers. It was extended only partially into the Lake Algonquin basin and there are no doubt many lakes in the area east of Georgian Bay containing one or more of these relict species. Lake Simcoe (Rawson, 1930) and Lake Nipissing (Langford, 1938) are also known to contain some of these forms. Dymond (1937) suggested that the presence of the smelt (*Osmerus mordax*) in Muskrat Lake (42) and Lake Doré was a result of the invasion of the Ottawa valley by the Champlain Sea.

Holmquist (1959) indicated that relict species originated from the elevation of ocean basins and their subsequent dilution by fresh water. As has been indicated, Ricker (1959) and Segerstråle (1962) agree relict distribution in North America has resulted from Pleistocene glaciation and proglacial lakes. The pattern of relict fauna distribution in the Algonquin Park area of Ontario would favour the latter hypothesis.

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Records of Mollusca from the Northwest Atlantic Obtained by Canadian Fishery Research Vessels, 1946–61[1]

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ABSTRACT

In the course of investigations into the fish and shrimp resources of an area from the southern edge of the Grand Bank and the Gulf of St. Lawrence to Cape Dyer, Baffin Island, numbers of Mollusca were taken. Commercial trawls were used for the great majority of the hauls and because of mesh selection most of the Mollusca taken were specimens of the larger species. The majority of the 45 species collected are well known and the value of the present list lies in the records of distribution from an area where climatic conditions have severely restricted past sampling endeavour.

INTRODUCTION

From 1946 to 1961, research vessels of the Fisheries Research Board of Canada, *Investigator II*, *Marinus*, and *A.T.Cameron*, and a chartered vessel *Fortune Breeze*, carried out numerous exploratory cruises the main object of which was to investigate the fish and shrimp resources off the eastern seaboard of Canada. The northern and southern limits of exploration were Cape Dyer, Baffin Island, and the south edge of the Grand Bank, respectively. In the course of these investigations, but incidental to them, numbers of Mollusca were obtained. Commercial trawls were mainly used in the investigations but these were often lined with small-mesh netting (approximately 1-inch mesh) in order to catch natant decapod crustacea. The result of this mesh selection was that most of the shells obtained were of a relatively large size — mostly more than 1 inch in length — thus the number of specimens and species is not particularly extensive. However, as the molluscan fauna of the region has been insufficiently studied it was thought valuable to publish the records with their geographical location and depth. In listing the records the numbers taken at each station are given in parentheses after the depth. It must be emphasized that the records are of *living* mollusca; dead shells are not included.

Figure 1 shows the positions of all hauls which collected living molluscs. Most of the hauls were taken at the edge of the continental shelf and on the slope at depths ranging between 80 and 1100 fath (1 fath = 1.83 m). Hydrographical data and geographical descriptions of the area are given by Hachey (1961) and Litvin and Rvachev (1962). No detailed synonymy of the species has been given but reference is given to sources listing previous records from this and adjacent areas and where necessary short comments on the specimens are given.

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Class AMPHINEURA

Family **Cryptochitonidae**

Symmetrogephyrus vestitus (Broderip & Sowerby)

NW Atlantic distribution: Arctic Ocean south to Massachusetts Bay, 3–30 fath (La Rocque, 1953).

New record: 51°19′N, 57°11′W, 52 fath, (1) (16–17 Oct. 50).

Cryptochitona abyssorum (M. Sars)

New record: 62°00′N, 60°40′W, 300 fath, (3) (1 Sept. 59).

This is the first record of this species from the Northwest Atlantic. Sars (1878) records it from off Stavanger, Norway, from 100–200 fath where it is associated with sponges. The present specimens measure 51, 53, 65 mm, respectively; Norwegian specimens have a maximum length of 34 mm.

Class BIVALVIA

Family **Nuculanidae**

Yoldia thraciaeformis (Storer)

NW Atlantic distribution: from 73°N off West Greenland, off Newfoundland, south to Massachusetts and in the Gulf of St. Lawrence 10–350 fath (La Rocque, 1953; Ockelmann, 1958; Nesis, 1962).

New records: 49°18′N, 52°03′W, 123 fath, (6) (22 Aug. 46); 55°42′N, 58°39′W, 248–258 fath, (3) (2 Aug. 60); 57°01′N, 59°31′W, 175 fath (1) (31 July 60).

The specimen taken at 57°N is probably the most northerly record off the Labrador coast, although the *Brisaster fragilis* community, of which it is a member, is truly arctic (Nesis, 1962) and *Yoldia thraciaeformis* probably extends further north still towards Baffin Island.

Family **Arcidae**

Bathyarca glacialis (Gray)

NW Atlantic distribution: West Greenland and from the Union Strait to the Gulf of St. Lawrence, 2–228 fath (La Rocque, 1953; Ockelmann, 1958; Clarke 1962a).

New record: 50°40′N, 53°30′W, 165 fath, (1) (4 Sept. 52).

Bathyarca pectunculoides (Scacchi)

NW Atlantic distribution: N Greenland and from Baffin Island south, 20–1810 fath (La Rocque, 1953; Ockelmann, 1958; Clarke, 1962a).

New record: 57°01′N, 59°31′W, 175 fath, (1) (31 July 60).

This is a polymorphous species, two fairly well-defined subspecies *A. p. grandis* and *A. p. septentricovalis* G.O.Sars have been described and this single specimen corresponds to the descriptions of the former (Ockelmann 1958).

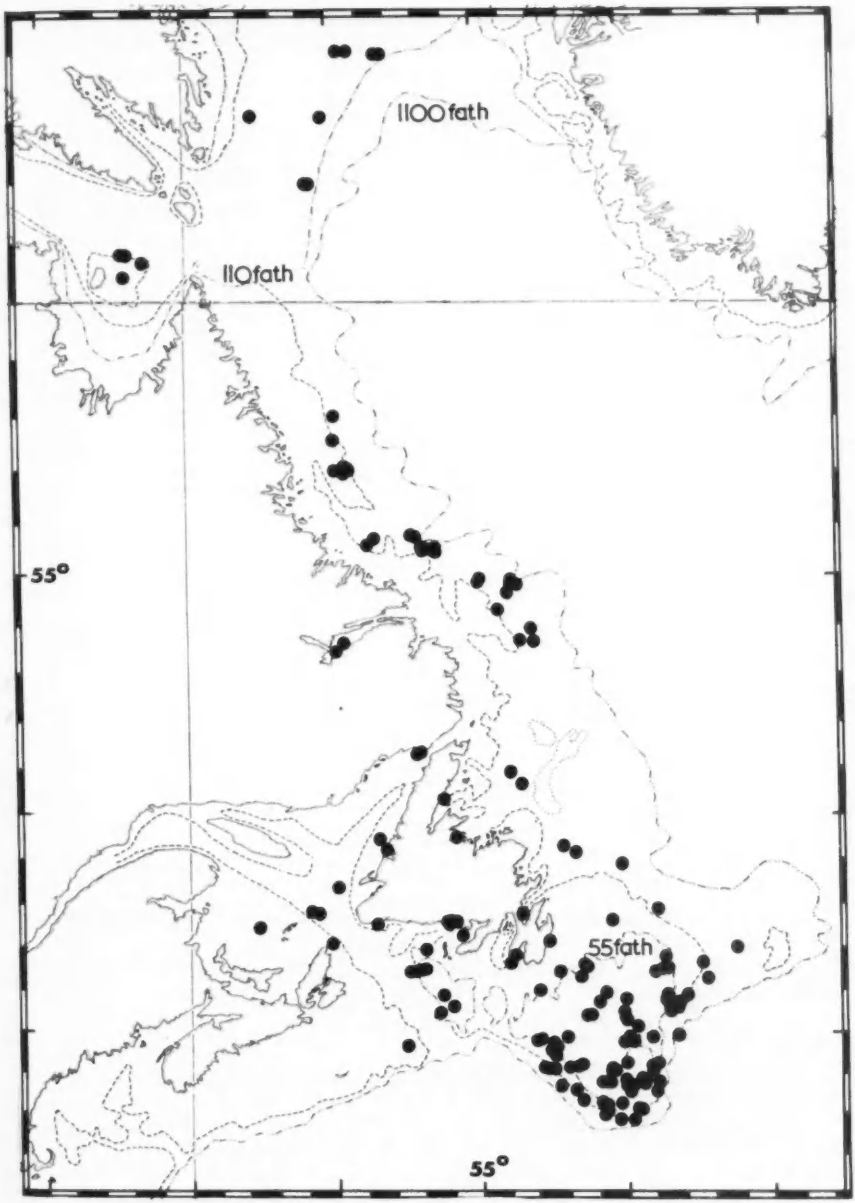

FIG. 1. Map showing the positions of those stations from which Mollusca were obtained.

Family **Pectinidae**

Chlamys islandicus (Müller)

NW Atlantic distribution: from Baffin Island and Labrador, south to Cape Cod in depths from a few feet to 202 fath (Ockelmann 1958; Clarke, 1962b).

New records (Fig. 2): 44°29′N, 52°05′W, 43 fath, (1) (29 Mar. 47); 48°22′N, 59°53′W, 115–125 fath, (1) (11 Nov. 47); 46°58′N, 56°57′W, 63–68 fath, (3) (23 Apr. 48); 44°45′N, 49°51′W, 30 fath, (16) (24 June 48); 51°19′N, 57°11′W, 40–50 fath, (1) (16 Oct. 50); 47°48′N, 60°47′W, 42 fath, (3) (9 Nov. 50); 45°46′N, 48°38′W, 48–55 fath, (4) (13 July 49); 46°33′N, 51°24′W, 44 fath, (1) (15 Apr. 51); 45°30′N, 48°28′W, 176 fath, (1) (11 July 51); 44°54′N, 48°12′W, 100 fath, (3) (13 July 51); 45°54′N, 48°35′W, 108 fath, (4) (11 July 51); 46°27′N, 57°19′W, 40 fath, (1) (30 June 52); 45°52′N, 56°20′W, 30 fath, (6) (1 June 53); 49°29′N, 58°28′W, 50 fath, (4) (3 Nov. 53); 46°20′N, 47°28′W, 116 fath, (1) (29 Aug. 51); 60°26′N, 67°00′W, 57 fath, (28) (9 May 59); 58°00′N, 59°52′W, 150–160 fath, (2) (10 Sept. 59); 63°01′N, 62°34′W, 125 fath, (1) (31 Aug. 59); 57°01′N, 59°31′W, 175 fath, (6) (31 July 60); 57°00′N, 59°38′W, 150 fath, (3) (1 Aug. 60); 55°27′N, 56°44′W, 126 fath, (1) (5 Aug. 60); 55°26′N, 56°29′W, 250 fath, (3) (4 Aug. 60); 55°27′N, 56°36′W, 187–205 fath, (5) (4 Aug. 60); 57°00′N, 59°38′W, 150 fath (5) (1 Aug. 60); 45°25′N, 51°21′W, 43 fath, (1) (20 June 61); 44°13′N, 48°53′W, 42 fath, (2) (24 June 61); 46°49′N, 48°39′W, 53 fath, (1) (29 June 61); 45°32′N, 48°16′W, 126 fath, (1) (28 June 61); 46°29′N, 57°05′W, 40 fath, (31) (date unknown).

This is the most common species in the collections and the new records extend the range of living *C. islandicus* to 250 fath.

Placopecten magellanicus (Gmelin)

NW Atlantic distribution: from the Strait of Belle Isle to North Carolina from less than 1 fath to 100 fath (Squires, 1962). Squires (1962) gives detailed distribution of this species in shallow waters around Newfoundland.

New records: 47°33′N, 56°08′W, 138 fath, (1) (12 June 58); 46°29′N, 57°05′W, 50 fath, (4) (date unknown).

Propeamussium groenlandicum (Sowerby)

NW Atlantic distribution: Baffin Island, NW Greenland and off Newfoundland 130–470 fath (La Rocque, 1953; Ockelmann, 1958).

New record: 43°39′N, 52°20′W, 400–415 fath, (4) (3 May 59).

Family **Mytilidae**

Musculus discors laevigata (Gray)

NW Atlantic distribution: from Baffin Island south to New York in 5–300 fath (La Rocque, 1953; Ockelmann, 1958).

New records: 44°29′N, 52°34′W, 54 fath, (1) (2 June 46); 60°26′N, 67°00′W, 60 fath, (2) (5 Sept. 59); 60°45′N, 67°02′W, 200 fath, (6) (6 Sept. 59).

Mytilus edulis Linnaeus

NW Atlantic distribution: Arctic Ocean to North Carolina intertidally and in shallow water only occasionally below 20 fath (La Rocque, 1953; Ockelmann, 1958).

New records: 45°34′N, 56°08′W, 25 fath, (1) (8 June 47); 43°09′N, 49°43′W, 39 fath, (3) (14 July 51); 53°37′N, 59°47′W, 14–16 fath, (33) (14 Oct. 52); 43°50′N, 49°35′W, 29 fath, (2) (23 June 61).

The collection of 33 from Lake Melville on the Labrador coast are very thin shelled and must be similar to those *M. edulis* collected by MacFarlane of the Hudson Bay Company in 1863 (Dall, 1919). These were some of the

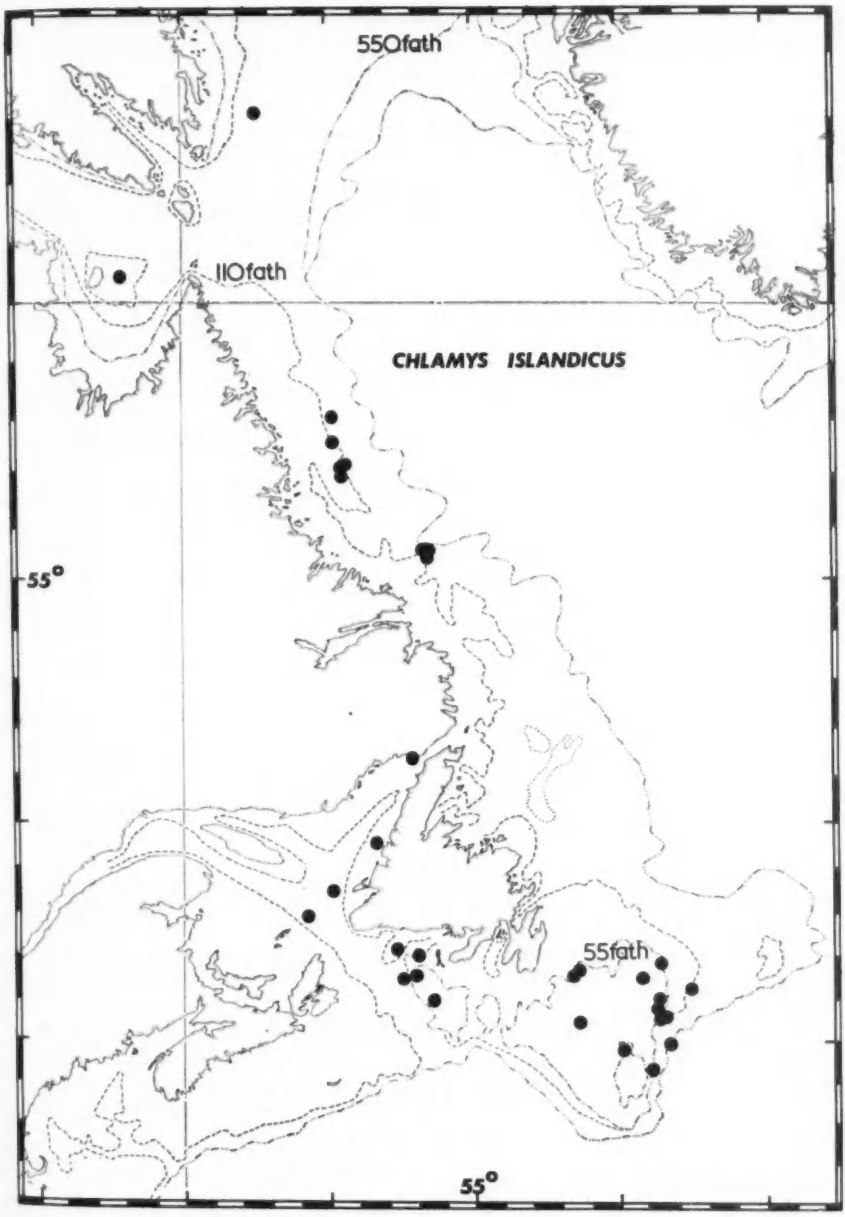

FIG. 2. Map showing the localities from which *Chlamys islandicus* was collected.

first molluscs ever collected from the Canadian Arctic at McKenzie Bay. Although this species is very common in high arctic waters the present records are of interest because they are from relatively deep water.

Family **Astartidae**

Astarte crenata acuticostata Jeffreys

NW Atlantic distribution: Greenland to Gulf of St. Lawrence 200–649 fath (La Rocque, 1953; Ockelmann, 1958).

New records: 64°00′N, 58°10′W, 298–400 fath, (7) (28 Aug. 59); 63°01′N, 60°10′W, 395 fath, (1) (30 Aug. 59).

Astarte crenata is a very variable species and although Ockelmann (1958) recognizes four subspecies he also records transitional forms between each. The above specimens are not typical and have been referred to the subspecies they most closely resemble.

Astarte crenata subaequilatera Sowerby

NW Atlantic distribution: Greenland to Florida, 22–410 fath (La Rocque, 1953; Ockelmann, 1958).

New records: 43°19′N, 50°58′W, 58 fath, (1) (1 June 46); 53°37′N, 59°47′W, 15 fath, (1) (14 Oct. 52); 47°33′N, 56°08′W, 138 fath, (2) (12 June 55); 57°01′N, 59°31′W, 175 fath, (1) (31 July 60); 57°00′N, 59°38′W, 150 fath, (1) (1 Aug. 60).

For comment see above subspecies.

Astarte sulcata (de Costa)

NW Atlantic distribution: SW Greenland, 5–470 fath (Ockelmann, 1958).

New records: 64°00′N, 58°10′W, 298–400 fath, (1) (28 Aug. 59); 54°46′N, 53°30′W, 310 fath, (1) (7 Aug. 60).

Family **Cyprinidae**

Cyprina islandica (Linnaeus)

NW Atlantic distribution: Arctic Ocean to North Carolina, 6–90 fath (Johnson, 1934) but Whiteaves (1901) states that it has not been found north of the Baie des Chaleurs in the Gulf of St. Lawrence (46°N).

New records: 44°29′N, 52°34′W, 65 fath, (2) (2 June 46); 44°13′N, 50°04′W, 29 fath, (1) (11 Mar. 52); 44°04′N, 50°35′W, 36 fath, (2) (22 June 61); 43°18′N, 50°14′W, 33 fath, (1) (23 June 61).

It seems likely that such a large species as *C. islandica* would have been collected by the extensive sampling of the research vessels of the Fisheries Research Board if it had occurred in latitudes higher than 46°N.

Family **Carditidae**

Venericardia borealis borealis (Conrad)

NW Atlantic distribution: Hudson Strait to Cape Hatteras, 3–250 fath (La Rocque, 1953).

New record: 56°59′N, 59°46′W, 100 fath, (2) (1 Aug. 60).

Venericardia borealis novangliae Morse

NW Atlantic distribution: Newfoundland to Cape Cod (La Rocque, 1953).

New record: 43°02′N, 50°41′W, 50 fath, (1) (23 June 61).

Verrill (1882) considered *V. novangliae* to be an inconsistent variety of *V. borealis* even though Morse (1869) had examined more than 130 specimens of the two species. Of these Morse distinguished 73 as *V. novangliae*. The present specimen is clearly identical to the excellent description given by Morse (1869) and differs so considerably from the specimens of *V. b. borealis* that re-examination of other material might show *V. b. novangliae* to be a valid species.

Family **Cardiidae**

Clinocardium ciliatum (Fabricius)

NW Atlantic distribution: Arctic Ocean to Cape Cod, 1–370 fath (La Rocque, 1953; Ockelmann, 1958).

New records: 46°51′N, 53°43′W, 55 fath, (1) (16 Dec. 46); 56°59′N, 59°46′W, 100 fath, (1. (1 Aug. 60); 55°29′N, 58°04′W, 78 fath, (2) (5 Aug. 60); 53°55′N, 53°07′W, 90 fath, (1) (10 Aug) 60); 55°25′N, 56°52′W, 106 fath, (2) (5 Aug. 60); 43°37′N, 48°57′W, 65 fath, (1) (24 June 61).

Cerastoderma pinnulatum (Conrad)

NW Atlantic distribution: Labrador to North Carolina, 2–80 fath (Whiteaves, 1901; Johnson, 1934).

New record: 54°35′N, 53°52′W, 200 fath, (1 dead) (19 Sept. 51).

Serripes groenlandicus Bruguiére

NW Atlantic distribution: Arctic Ocean to Cape Cod, 2–165 fath (La Rocque, 1953; Ockelmann, 1958).

New records: 43°45′N, 50°44′W, 37 fath, (2) (11 May 52); 43°37′N, 48°57′W, 65 fath, (1) (24 June 61).

Family **Tellinidae**

Macoma balthica (Linnaeus)

NW Atlantic distribution: Arctic Ocean to Georgia, at or a little below L.W.M. in Canadian waters (La Rocque, 1953).

Many from intertidal sand at St. John's Island, Lake Melville (54°N) (15 Oct. 52).

Macoma calcarea (Gmelin)

NW Atlantic distribution: Arctic Ocean to Long Island Sound, 5–370 fath (Whiteaves, 1901; La Rocque, 1953; Ockelmann, 1958).

New record: 57°00′N, 59°38′W, 150 fath, (2) (1 Aug. 60).

Although this species is common in the Northwest Atlantic, it is not usually taken below 80 fath.

Family **Mactridae**

Spisula polynema Stimpson

NW Atlantic distribution: Hudson Bay to Georges Bank, Massachusetts, L.W.M.–60 fath (La Rocque, 1953; Abbot, 1954).

New record: 45°19′N, 50°02′W, 33 fath, (1) (11 May 53).

Chamberlin and Stearns (1963) list in considerable detail the known and probable distribution of this species and relate the distribution to the physical environment. This record, from the Grand Bank, is from a region postulated as suitable for the survival and the reproduction of *S. polynema*.

Family **Mesodesmatidae**

Mesodesma arctatum (Conrad)

NW Atlantic distribution: Gulf of St. Lawrence to New Jersey, L.W.M.–50 fath (Gould, 1870; La Rocque, 1953; Abbot, 1954).

New record: 43°50′N, 50°05′W, 29 fath, (4) (23 June 47).

Whiteaves (1901) discusses differences between *Mesodesma arctatum* and *M. deauratum* and although not convinced that they are separate species, states that all the Canadian specimens that he had seen agreed better with the figure of *M. arctatum* as illustrated in Gould (1870). This is true of the present specimens.

Family **Saxicavidae**

Cyrtodaria siliqua (Spengler)

NW Atlantic distribution: Arctic Ocean to Georges Bank, 5–90 fath (La Rocque, 1953; Abbot, 1954).

New records (Fig. 3): Many of the specimens were taken from the stomach contents of fish, notably cod and American plaice. These records are marked with an asterisk. 45°28′N, 49°06′W, 40–50 fath, (3) (22 July 49)*; 46°39′N, 54°00′W, 25 fath, (1) (2 Sept. 46)*; 43°40′N, 50°00′W, 31 fath, (1) (5 May 47); 43°41′N, 50°43′W, 35–40 fath, (4) (17 May 47)*; 46°23′N, 52°20′W, 41–47 fath, (2) (7 July 47); 48°52′N, 50°10′W, 120–127 fath, (2) (26 Sept. 47); 45°40′N, 48°13′W, 35–60 fath, (1) (6 July 48)*; 46°58′N, 56°57′W, 63–68 fath, (2) (23 Apr. 48); 45°48′N, 50°03′W, 33–34 fath, (1) (17 July 48); 44°49′N, 53°00′W, 46–50 fath, (1) (22 May 49); 45°40′N, 48°13′W, 95–98 fath, (2) (13 July 49)*; 43°05′N, 49°40′W–42°50′N, 49°45′W, 110–205 fath, (2) (10 Dec. 49)*; 47°48′N, 60°44′W, 56–60 fath, (1) (9 Nov. 50); 44°09′N, 51°42′W, 45 fath, (3) (26 Apr. 52); 47°28′N, 62°39′W, 33 fath, (3) (10 Nov. 50)*; 43°45′N, 50°44′W, 37 fath, (9) (11 May 52); 47°38′N, 50°33′W, 82 fath, (19) (19 June 52)*; 44°47′N, 53°32′W, 48–55 fath, (7) (17 Feb. 53)*; 49°09′N, 51°45′W, 40 fath, (1) (7 May 53); 45°41′N, 51°00′W, 44 fath, (8) (7 May 53)*; 45°19′N, 50°02′W, 33 fath, (2) (11 May 53); 44°04′N, 50°35′W, 36 fath, (1) (22 June 61).

No specimens of the closely related *C. kurriana* were taken and it is doubtful if this latter species occurs in the area investigated, although it is present off West Greenland (La Rocque, 1953; Ockelmann, 1958). No specimens of *C. siliqua* were taken in latitudes higher than 50°N.

Hiatella arctica (Linnaeus)

NW Atlantic distribution: Arctic Ocean to Panama, 1–100 fath (La Rocque, 1953; Ockelmann, 1954).

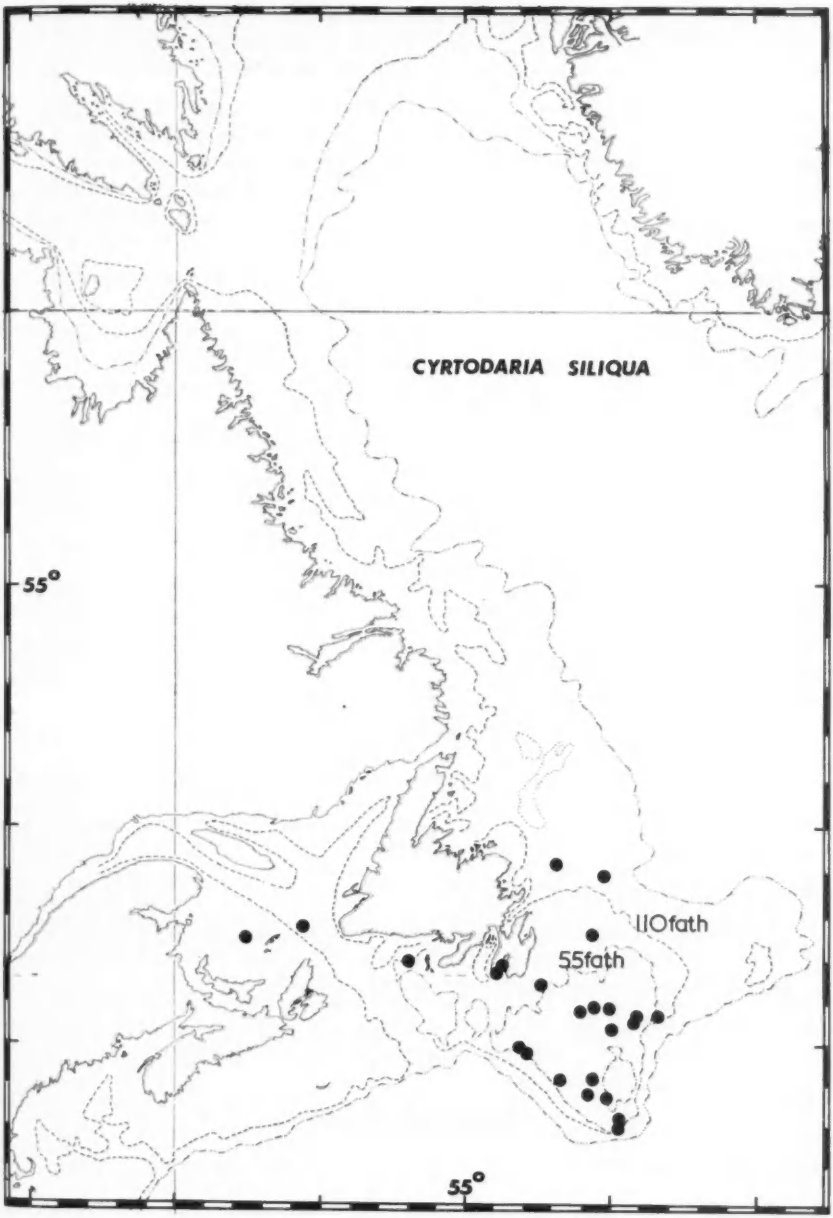

FIG. 3. Map showing the localities from which *Cyrtodaria siliqua* was collected.

New records: 43°35′N, 51°34′W, 49 fath, (1) (31 May 46); 45°34′N, 56°08′W, 25 fath, (1) (8 June 47); 43°44′N, 49°30′W, 28–40 fath, (3) (24 Apr. 51); 44°45′N, 50°08′W, 31 fath, (3) (8 May 52); 53°37′N, 59°47′W, 16 fath, (1) (14 Oct. 52); 55°28′N, 56°35′W, 180 fath, (2) (4 Aug. 60); 43°50′N, 49°35′W, 29 fath, (3) (23 June 61); 45°06′N, 49°05′W, 36 fath, (1) (26 June 61).

Although *H. arctica* is one of the most common species of bivalve in arctic seas it should be noted that two living specimens were collected from 180 fath. Although it is reported to extend into deep water in the warmer parts of the large oceans (Ockelmann, 1958) there are few records of living animals below 100 fath, presumably because there is a lack of suitable surfaces for attachment at great depths.

Family **Pholadidae**

Xylophaga atlanticus Richards

NW Atlantic distribution: from off Quebec to Virginia from floating or waterlogged wood 50–2033 fath (Turner, 1955; Clarke, 1962a).

New record: 47°15′N, 55°43′W, 102 fath (many in a submerged block of timber) (26 Nov. 52).

This is the fourth record from Canadian waters since it was first described by Richards (1942). For other records see Turner (1955) and Clarke (1962a).

Family **Cuspidariidae**

Cuspidaria obesa (G. O. Sars)

NW Atlantic distribution: Arctic Ocean to West Indies, 10–2435 fath (La Rocque, 1953, Ockelmann, 1958; Clarke 1962a).

New record: 47°33′N, 56°08′W, 135 fath, (2) (12 June 55).

Class SCAPHOPODA

Family **Dentaliidae**

Dentalium occidentale Stimpson

NW Atlantic distribution: Gulf of St. Lawrence to Cape Hatteras 50–1686 fath (Whiteaves, 1901; La Rocque, 1953).

New record: 47°33′N, 56°08′W, 135 fath, (2) (12 June 55).

Class GASTROPODA

Family **Lepetidae**

Lepeta coeca (Müller)

NW Atlantic distribution: Arctic Ocean to Massachusetts, 2–700 fath (Thorson, 1944; La Rocque, 1953).

New record: 64°00′N, 58°10′W, 300–400 fath, (3) (28 Aug. 59).

Family **Naticidae**

Polinices pallidus (Broderip & Sowerby)

NW Atlantic distribution: Arctic Ocean to Cape Hatteras, 3–1370 fath (Whiteaves, 1901; Thorson, 1944; La Rocque, 1953).

New records: 44°04′N, 50°35′W, 38 fath, (1) (22 June 61); 45°32′N, 48°32′W, 60 fath, (1) (28 June 61).

Polinices heros (Say)

NW Atlantic distribution: Gulf of St. Lawrence to North Carolina, 1–238 fath (La Rocque, 1953).

New record: 44°38′N, 57°47′W, 18 fath, (2) (7 July 46).

Family **Trichotropidae**

Trichotropis bicarinata Broderip & Sowerby

NW Atlantic distribution: Arctic Seas and West Greenland, 10–270 fath (Thorson, 1951; La Rocque, 1953).

New record: 64°01′N, 59°28′W, 208 fath, (2) (29 Aug. 59).

This is a rare species. There are two previous records from waters adjacent to those sampled in the present investigation (Thorson, 1951). One of these specimens has been drawn by Winther (Thorson, 1951) and the present specimens are very similar to it.

Family **Aporrhaidea**

Aporrhais occidentalis Beck

NW Atlantic distribution: Labrador to North Carolina, 5–1000 fath (La Rocque, 1953; Clarke, 1962a, b).

New records (Fig. 4): 45°56′N, 52°58′W, 50 fath, (2) (26 June 47); 44°25′N, 52°27′W, 50 fath, (1) (17 May 48); 46°33′N, 51°24′W, 44 fath, (1) (15 Apr. 51); 44°55′N, 49°12′W, 140 fath, (1) (10 July 51); 50°55′N, 53°57′W, 165 fath, (3) (3 Sept. 52); 54°52′N, 55°02′W, 112 fath, (1) (8 Aug. 60); 44°13′N, 51°35′W, 42 fath, (1) (21 June 61); 43°48′N, 50°52′W, 40 fath, (2) (20 June 61); 43°02′N, 50°41′W, 50 fath, (1) (23 June 61); 43°29′N, 49°09′W, 62 fath, (1) (24 June 61).

Johnson (1930) distinguished three varieties of this species. The present specimens show intergrading characters so that it is not possible to refer them to a particular variety.

Family **Muricidae**

Trophon craticulatus (Fabricius)

NW Atlantic distribution: Hudson Strait to Newfoundland Banks, 30–80 fath (Thorson, 1944; La Rocque, 1953).

New record: 45°25′N, 51°21′W, 43 fath, (2) (20 June 61).

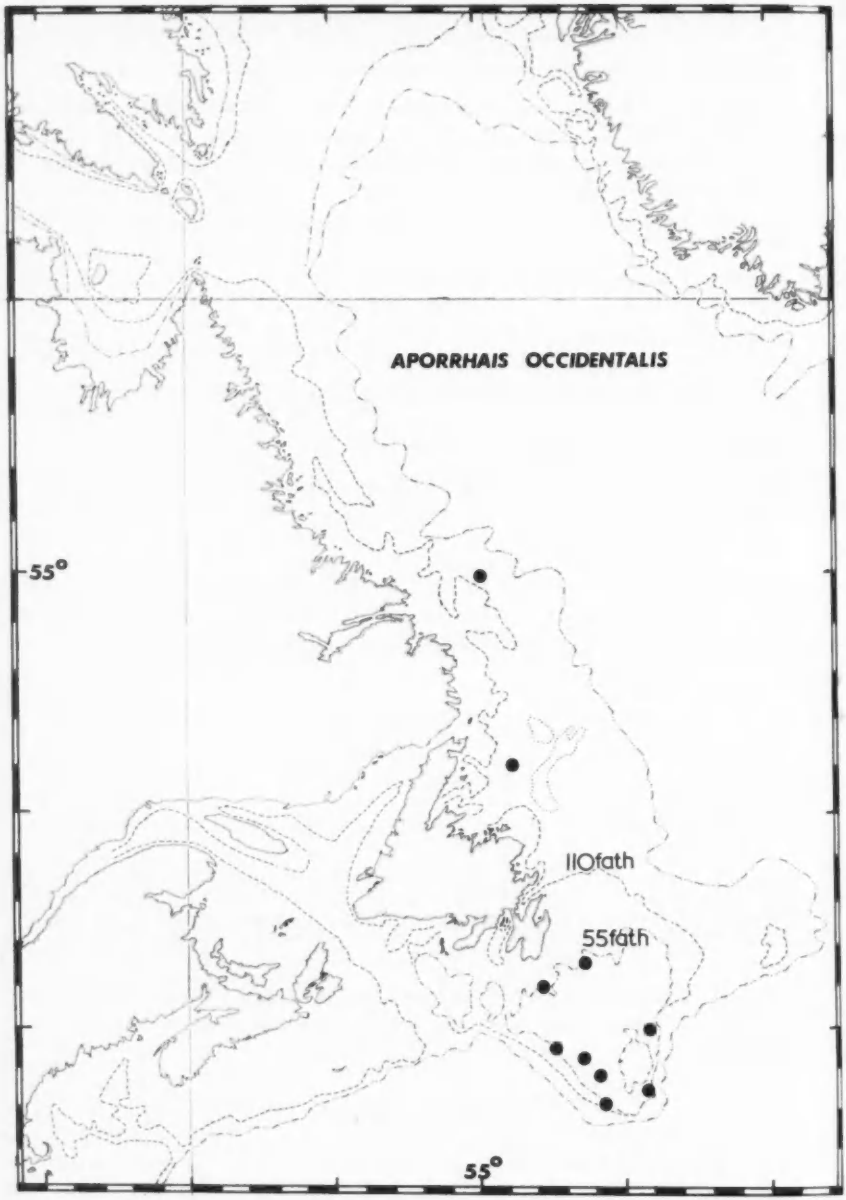

FIG. 4. Map showing the localities from which *Aporrhais occidentalis* was collected.

Family **Buccinidae**

Buccinum undatum Linnaeus (Fig. 9a)

NW Atlantic distribution: Labrador to New Jersey, L.W.M.–170 fath (Whiteaves, 1901; La Rocque, 1953).

New records: 47°39′N, 55°43′W, 110–150 fath, (1) (16 Dec. 53); 47°33′N, 58°35′W, 105 fath, (2) (31 July 47); 55°40′N, 57°19′W, 162–175 fath, (1) (31 Aug. 50); 55°40′N, 57°08′W, 180 fath, (1) (31 Aug. 50); 46°33′N, 48°46′W, 39 fath, (1) (15 July 51).

Many of the species of *Buccinum* from the Northwest Atlantic are extraordinarily difficult to identify with certainty, for there are so many intergrades of form. This variation has led to a multiplicity of descriptions of new species (see La Rocque, 1953, for a list) and it is evident from the literature that many are synonymous (e.g. Whiteaves, 1901; Stimpson, 1865; Thorson, 1944 and 1951) and that a revision of the family is urgently required.

The above specimens that have been identified as *B. undatum* are much lighter and much less heavily ornamented than the European species. Although mindful of such comments as those of Dawson, quoted by Whiteaves (1901), on the differences between the various species of *Buccinum* reference to specimens of this species from the NW Atlantic confirms their identification (Fig. 9).

Buccinum hydrophanum Hancock (Fig. 9b)

NW Atlantic distribution: NW Greenland, Labrador to Grand Banks, 2–470 fath (Thorson, 1944, 1951; La Rocque, 1953).

New records (Fig. 5): 44°08′N, 52°05′W, 49 fath, (1) (15 May 46); 44°53′N, 49°58′W, 29 fath, (1) (18 Aug. 49); 43°10′N, 50°43′W, 48 fath, (1) (21–26 Apr. 51); 43°44′N, 49°30′W, 28–40 fath, (1) (24 Apr. 51); 43°09′N, 49°43′W, 38 fath, (1) (14 July 51); 43°38′N, 51°36′W, 47 fath, (1) (9 May 52); 43°32′N, 51°42′W, 68 fath, (3) (10 May 52); 50°55′N, 53°57′W, 150 fath, (1) (3 Sept. 52); 64°01′N, 59°28′W, 208 fath, (2) (29 Aug. 59); 53°40′N, 53°06′W, 125 fath, (3) (11 Aug. 60); 44°13′N, 51°35′W, 42 fath, (10) (21 June 61); 43°50′N, 49°35′W, 29 fath, (4) (23 June 61); 44°32′N, 52°31′W, 48 fath, (1) (20 June 61); 43°30′N, 49°55′W, 30 fath, (8) (23 June 61); 43°29′N, 49°09′W, 55–70 fath, (3) (24 June 61); 44°13′N, 48°53′W, 40 fath (3) (24 June 61); 43°18′N, 50°14′W, 60 fath, (1) (24 June 61); 55°25′N, 56°52′W, 106 fath, (1) (5 Aug. 60); 55°31′N, 58°47′W, 410 fath, (2) (2 Aug. 60).

Thorson (1951) states that this is a pronounced arctic species, migrating to shallow water in high latitudes, but further south occurring only at greater depths. The present records (Fig. 5) show that it extends to the outer edge of the Grand Banks but it appears to be restricted to the edge of the continental slope in Newfoundland waters.

Buccinum tenue Gray (Fig. 9c)

NW Atlantic distribution: Labrador to Gulf of Maine, 42–92 fath (Thorson, 1951; La Rocque, 1953).

New record: 44°04′N, 50°35′W, 38 fath, (1) (22 June 61).

Buccinum totteni Stimpson (Fig. 9d)

NW Atlantic distribution: Labrador to Gulf of St. Lawrence, 8–50 fath (Whiteaves, 1901; La Rocque, 1953).

New records (Fig. 5): 45°29′N, 50°08′W, 35 fath, (1) (18 Aug. 49); 43°44′N, 49°30′W, 28–40 fath, (2) (24 Apr. 51); 43°32′N, 51°42′W, 68 fath, (2) (10 May 51); 62°00′N, 60°40′W,

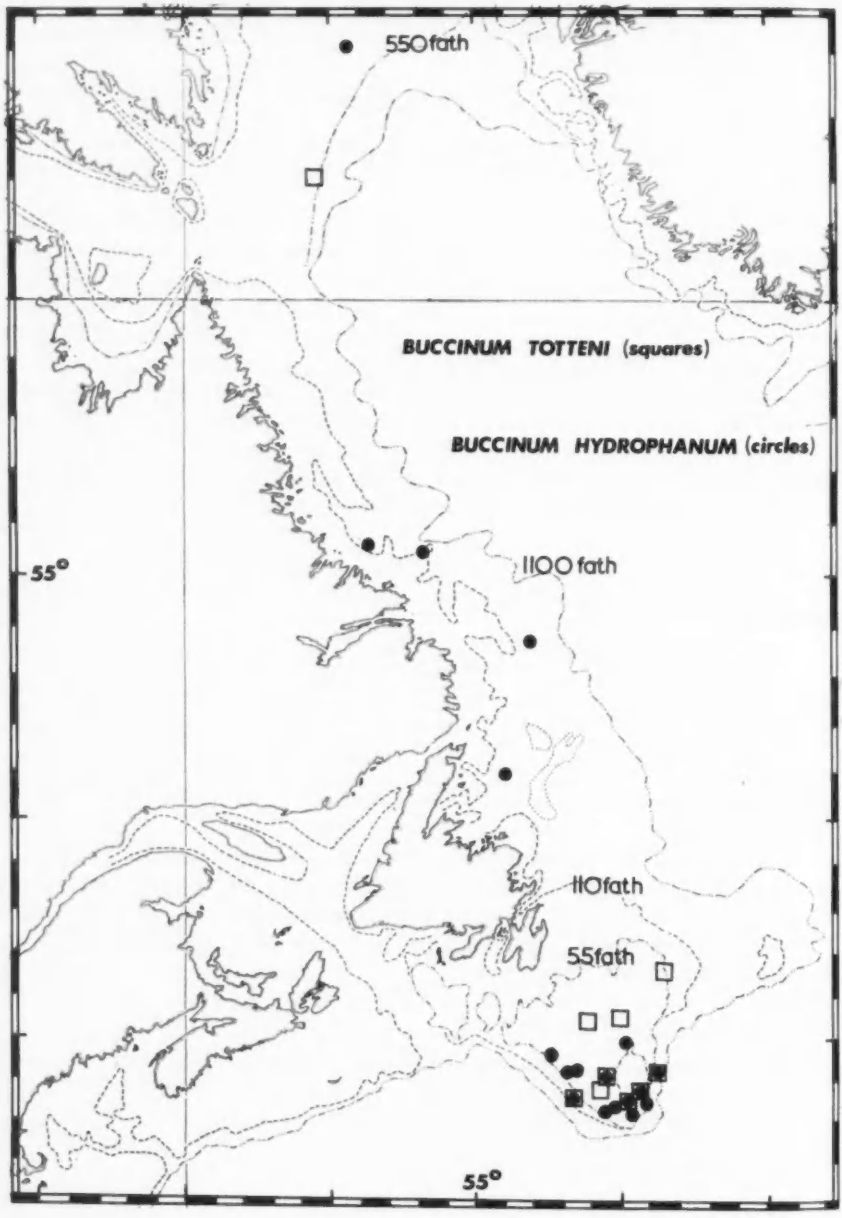

FIG. 5. Map showing the localities from which *Buccinum totteni* and *B. hydrophanum* were collected.

300 fath, (1) (1 Sept. 59); 44°04′N, 50°35′W, 48 fath, (3) (20 June 61); 45°25′N, 51°21′W, 43 fath, (2) (20 June 61); 43°48′N, 50°52′W, 40 fath, (1) (20 June 61); 43°30′N, 49°55′W, 31 fath, (2) (23 June 61); 44°13′N, 48°53′W, 40 fath, (3) (24 June 61); 45°32′N, 48°32′W, 60 fath, (4) (28 June 61).

The record from 62°N considerably increases the depth range of this species.

Family **Neptunidae**

Neptunea despecta (Linnaeus)

NW Atlantic distribution: La Rocque (1953) records it from "Gulf of St. Lawrence to off south of Martha's Vineyard, 10–471 fath," but it is clear from Thorson (1944, 1951) and Golikov (1963) that this is a circumpolar arctic species and the latter authors give Labrador in their localities. Labrador is therefore confirmed by present records.

New records (Fig. 6): 44°29′N, 52°34′W, 50 fath, (2) (2 June 46); 44°51′N, 47°30′W, 66 fath, (5) (7 July 46); 55°40′N, 57°19′W, 140 fath, (1) (31 Aug. 50); 54°14′N, 54°15′W, 108 fath, (1) (18 Sept. 51); 44°03′N, 52°37′W, 230–360 fath, (1 dead shell) (17 July 63); 54°45′N, 53°50′W, 175 fath, (1) (6 Aug. 60); 54°52′N, 55°02′W, 112 fath, (1) (8 Aug. 60); 44°04′N, 50°35′W, 38 fath, (1) (22 June 61); 43°48′N, 50°52′W, 40 fath, (1) (20 June 61); 43°37′N, 48°57′W, 65 fath, (1) (24 June 61).

Volutopsis largillierti (Petit de la Saussaye)

NW Atlantic distribution: Gulf of St. Lawrence and Newfoundland, 50 fath (La Rocque, 1953), West Greenland, 70–160 fath (Thorson, 1951).

New records: 54°50′N, 53°48′W, 200 fath (1) (6 Sept. 50); 44°11′N, 49°03′W, 120 fath, (1) (9 July 51); 44°11′N, 59°05′W, 100 fath, (2) (9 July 51); 46°04′N, 48°12′W, 62 fath, (4) (22 June 53); 46°16′N, 47°13′W, 250 fath, (1) (19 July 59).

The above specimens extend the range and depth of this species in Canadian waters. They also differ from the normal form in having one less nuclear whorl.

Colus spitzbergensis (Reeve)

NW Atlantic distribution: Labrador to Gulf of St. Lawrence, 1–142 fath (La Rocque, 1953).

New records (Fig. 7): 47°45′N, 53°35′W, 130 fath, (1) (10 Oct. 47); 44°31′N, 52°39′W, 50 fath, (1) (18 May 48); 49°29′N, 56°04′W, 175 fath, (1) (29 Oct. 51); Notre Dame Bay, 32 fath, (1) (14 Nov. 51); 44°45′N, 50°08′W, 31 fath, (an eggmass) (8 May 52); 60°40′N, 66°21′W, 300 fath, (one plus an eggmass) (4 Sept. 59); 54°46′N, 53°30′W, 300 fath, (1) (7 Aug. 60); 55°25′N, 56°52′W, 106 fath, (3) (5 Aug. 60); 44°32′N, 52°31′W, 48 fath, (1) (20 June 61).

Colus stimpsoni (Mörch)

NW Atlantic distribution: Labrador to North Carolina, 1–471 fath (La Rocque, 1953).

New records (Fig. 7): 44°29′N, 52°34′W, 50 fath, (2) (2 June 46); 47°53′N, 48°57′W, 125 fath, (1) (21 Sept. 49); 44°31′N, 52°39′W, 50 fath, (1) (18 May 48); 54°50′N, 53°48′W, 200 fath, (1) (6 Sept. 50); 46°35′N, 47°22′W, 142 fath, (2) (14 July 51); 46°16′N, 47°13′W, 250 fath, (1) (19 July 59); 43°37′N, 48°57′W, 65 fath, (1) (24 June 61); 45°32′N, 48°16′W, 126 fath, (1) (28 June 61).

Colus ventricosus (Gray)

NW Atlantic distribution: Nova Scotia to Georges Bank (La Rocque, 1953).

New records: 43°05′N, 49°40′W, 105–225 fath, (1) (10 Dec. 49); 43°44′N, 49°30′W, 35 fath, (1) (24 Apr. 51); 43°18′N, 50°14′W, 35 fath, (1) (23 June 61).

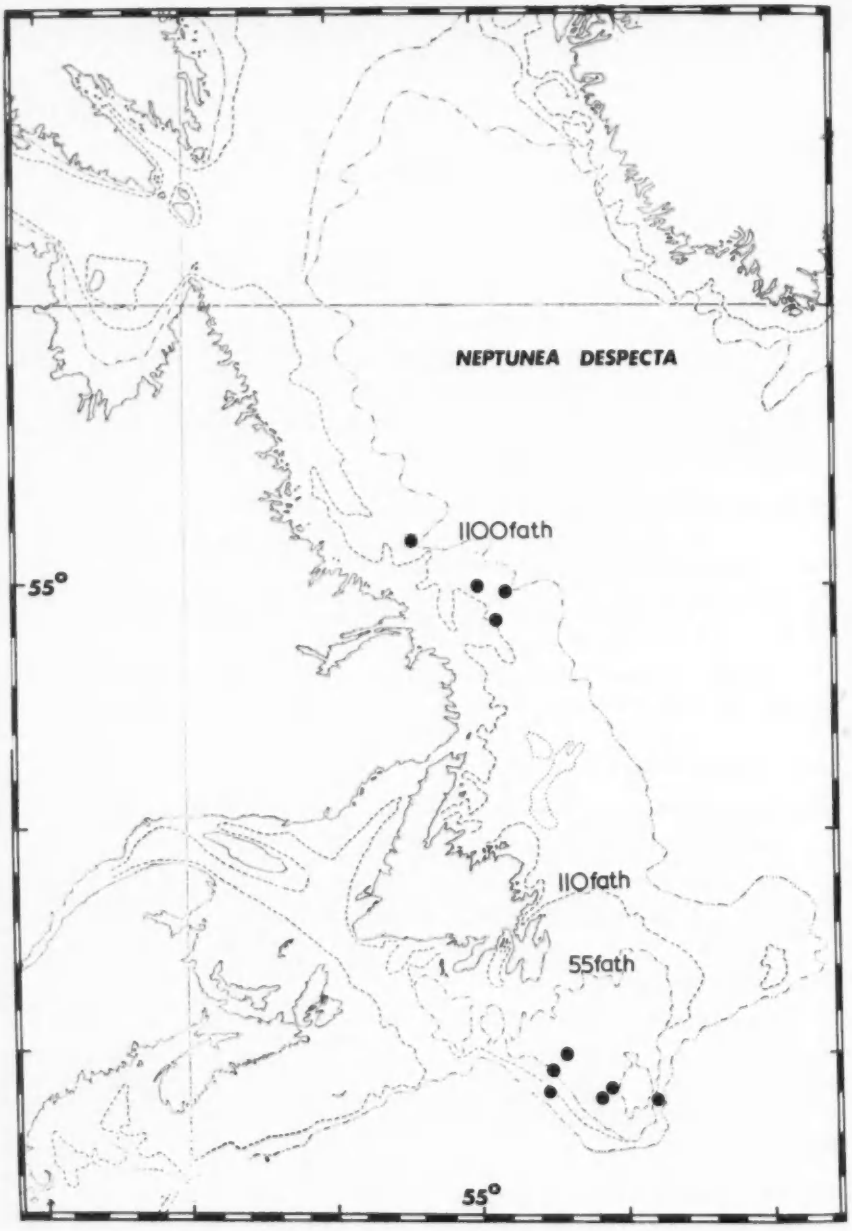

FIG. 6. Map showing the localities from which *Neptunea despecta* was collected.

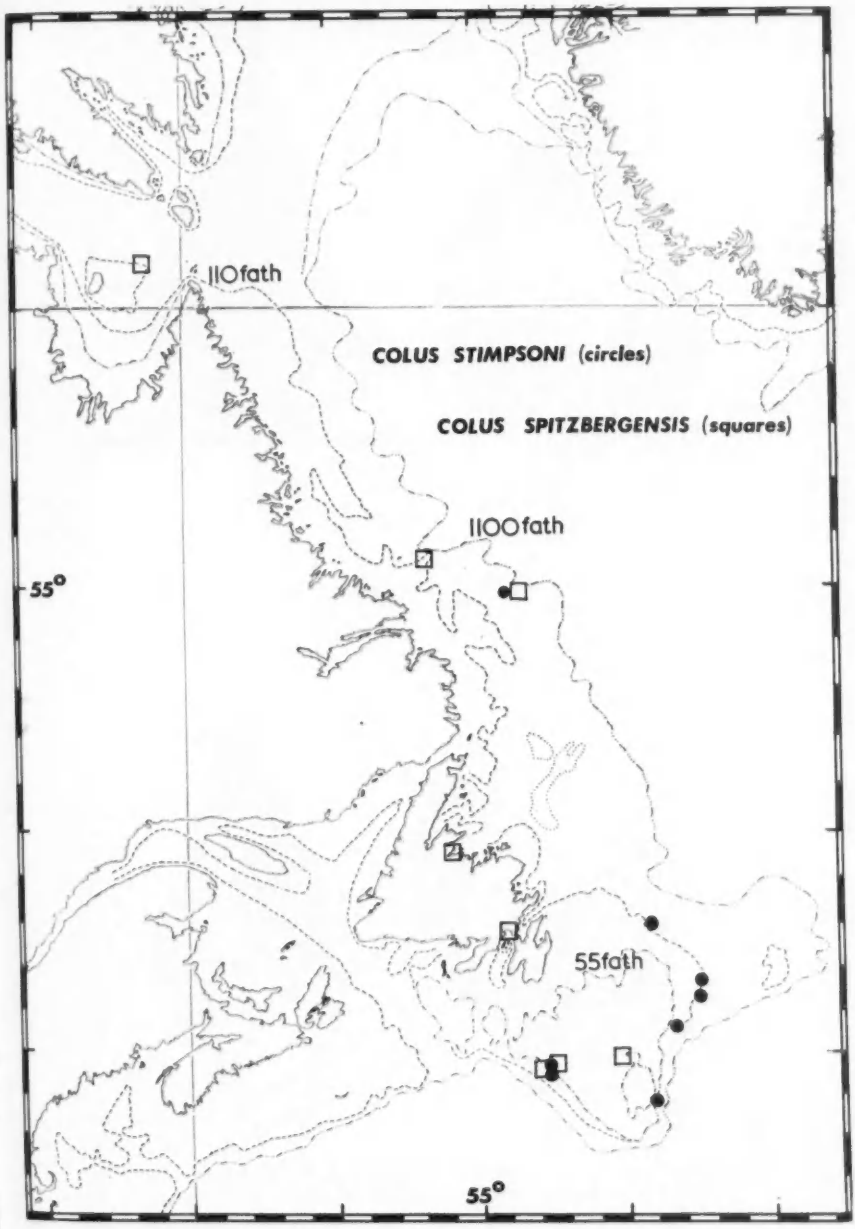

FIG. 7. Map showing the localities from which *Colus stimpsoni* and *C. spitzbergensis* were collected.

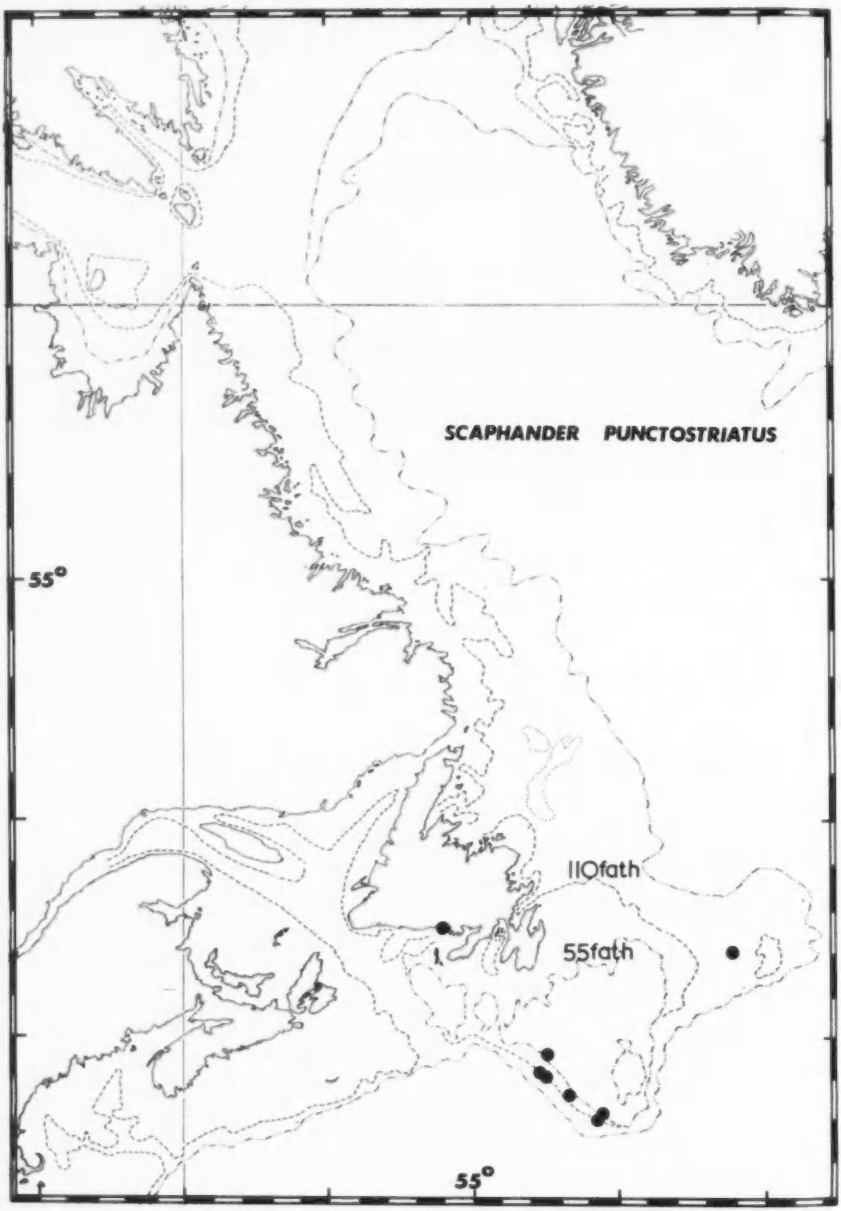

FIG. 8. Map showing the localities from which *Scaphander punctostriatus* was collected.

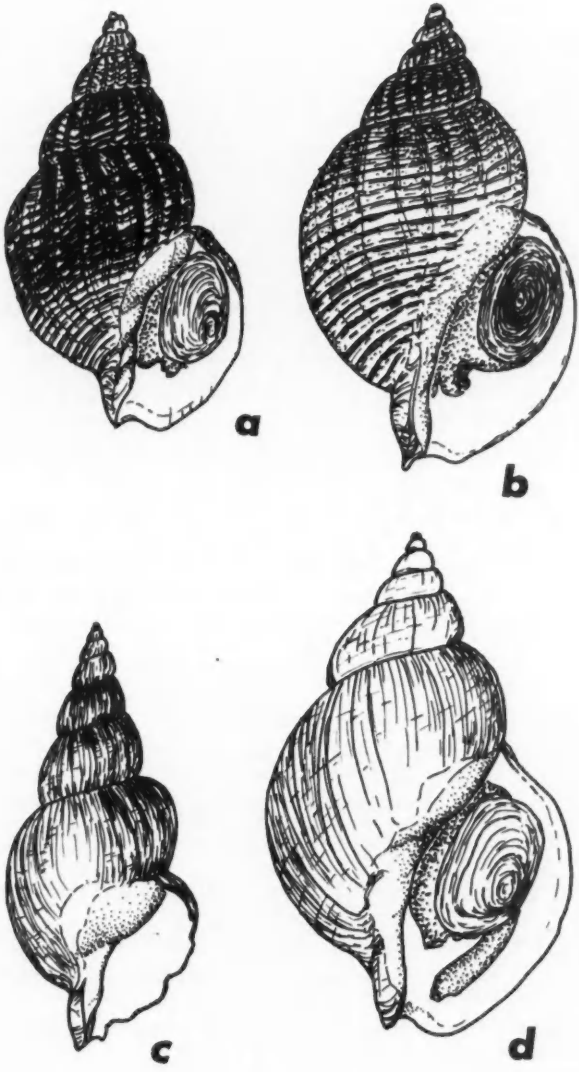

FIG. 9. External morphological features of *Buccinum* species: (a) *Buccinum undatum*; (b) *Buccinum hydrophanum*; (c) *Buccinum tenue*; (d) *Buccinum toteni*.

Family **Scaphandridae**

Scaphander punctostriatus (Mighels)

NW Atlantic distribution: Gulf of St. Lawrence to West Indies, 46–1476 fath (La Rocque, 1953).

New records (Fig. 8): 44°08′N, 52°50′W, 95 fath, (1) (9 Mar. 51); 47°00′N, 46°10′W, 170 fath, (1) (26 Aug. 51); 43°32′N, 51°42′W, 68 fath, (4) (10 May 52); 44°03′N, 52°37′W, 230–360 fath, (4) (17 July 53); 44°32′N, 52°31′W, 48 fath, (1) (20 June 61); 42°56′N, 50°50′W, 80 fath, (2) (23 June 61); 43°02′N, 50°41′W, 50 fath, (1) (23 June 61).

Family **Dendronotidae**

Dendronotus frondosus Ascanius

NW Atlantic distribution: Labrador to Rhode Island, 4–60 fath (La Rocque, 1953), West Greenland (Lemche, 1941).

New records: 44°44′N, 53°08′W, 55–65 fath, (2) (6 July 47); 47°07′N, 52°41′W, 85 fath, (1) (13 Sept. 49); 45°54′N, 47°53′W, 160 fath, (1) (13 July 51); 50°21′N, 56°19′W, 150 fath, (5) (5 Oct. 51); 47°06′N, 60°08′W, 112 fath, (1) (2 Nov. 52); 44°13′N, 48°53′W, 41 fath, (1) (24 June 61); 43°20′N, 51°31′W, 65 fath, (7) (9 July 61).

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Movements of Hatchery-Reared Lake Trout in Lake Superior[1,2]

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ABSTRACT

The history of stocking of lake trout (*Salvelinus namaycush*) in the Great Lakes is reviewed.

The study of movements is based on capture of 24,275 fin-clipped lake trout taken in experimental gill nets and trawls and commercial gill nets.

Yearling lake trout planted from shore dispersed to 15-fath (27-m) depths in 3½ hr. Most fish remained within 2 miles (3.2 km) of the planting site 2 months, but within 4 months some fish had moved as much as 17 miles (27 km). The highest abundance of planted lake trout was in areas 2–4 miles (3.2–6.4 km) from the planting site even 3 years after release. Distance moved and size of fish were not correlated.

Dispersal of lake trout begins at planting and probably continues until the fish are mature. Most movement was eastward in southern Lake Superior and followed the counterclockwise surface currents. Movement is most rapid in areas of strong currents and slowest in areas of weak currents or eddies. Movement to areas west of the Keweenaw Peninsula was insignificant from plantings in Keweenaw Bay and nil from other plantings farther east. Lake trout planted in the eastern third of the lake dispersed more randomly than those planted farther west. Few fish moved farther offshore than the 50-fath (91-m) contour. Lake trout planted in Canadian waters made insignificant contributions to populations in US waters.

INTRODUCTION

Prior to the mid 1930s, millions of lake trout (*Salvelinus namaycush*) fry were stocked annually in the Great Lakes in the belief that, somehow, hatchery production was superior to natural reproduction. Lake trout stocking was largely abandoned in the 1930s because evidence of effectiveness of the practice was lacking (Dymond, 1957). The extreme reduction or near extinction of lake trout stocks caused by depredations of the sea lamprey (*Petromyzon marinus*) in the upper Great Lakes forced reconsideration of stocking as a method of maintaining abundance or of re-establishing populations. Because potential sources of lake trout eggs in inland lakes were either small or were in remote areas, stocking of millions of fry could no longer be considered. Attention was directed, therefore, to rearing lake trout to sizes or ages where chances of

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survival might be good. A series of large-scale experimental plantings, most of which involved interagency co-operation, was begun in 1944 and has continued to the present.

By the late 1950s, experimental plantings of 9- to 37-month-old lake trout indicated that fish 16–18 months old should yield the highest survival consistent with rearing costs. So long as the sea lamprey was uncontrolled, no reliable information could be obtained on average survival rates — only relative survival of fish planted at various sizes or ages was known. Nevertheless, the critical state of the fishery and the lake trout population in Lake Superior demanded intensive stocking as soon as a means of controlling the sea lamprey was available.

The discovery of a chemical that selectively kills all year-classes of sea lamprey larvae in the streams, and the decision of the Great Lakes Fishery Commission to begin treatment in 1958 of all lamprey-producing streams tributary to Lake Superior, improved greatly the prospects for profitable stocking. Rearing and planting of yearling lake trout were intensified. The Michigan Department of Conservation had developed methods of holding lake trout brood stock and was able to supply enough eggs for the rearing facilities of all US agencies by 1962. Increased research by both Canadian and US agencies included evaluation of the success of stocking as one of the principal objectives.

In 1947–61, a total of 5,730,000 fin-clipped lake trout was planted in Lake Superior in a total of 51 separate plantings. Of these, slightly over 1 million were fingerlings planted in the fall (most of the fingerlings were planted prior to 1955) and about 50,000 were 2- or 3-year-old fish. The remainder were yearlings, 15–17 months old, planted in the spring. Prior to 1960, most of the fish were planted from boats in water 15–20 fath deep within a few miles of shore. Few plantings in US waters were spread over wide areas. A few Canadian plantings were made from aircraft. In 1960, two large plantings were released directly from shore in areas within 1 mile of water 15 fath deep. Since 1960, nearly all plantings in US waters have been released from shore. Prior to 1956, some fin marks were repeated in consecutive years, but since then no mark has been used more than once in 2 years.

Knowledge of the movements of planted lake trout is necessary for evaluation of survival of planted fish or of the relative success of various planting practices. Because the objective of stocking lake trout is to re-establish naturally reproducing populations in all areas formerly occupied by lake trout in the Great Lakes, the extent of movement may determine where lake trout must be planted. This report reviews earlier studies on movements of marked lake trout, both hatchery-reared and native in the Great Lakes, summarizes the studies on dispersal of small planted lake trout done by the Bureau of Commercial Fisheries research vessel *Siscowet*, and describes the movements of lake trout planted at various locations in US waters of Lake Superior in 1952–61.

MATERIALS AND METHODS

This study is based on 436 fin-clipped lake trout caught in experimental gill nets, 2338 captured in experimental trawls, and 21,501 taken in 4½-inch-mesh (114-mm), extension measure, gill nets by commercial fishermen. The gear was not specified for 52 fish from north shore and offshore waters of Ontario.

Using the research vessel *Siscowet*, we obtained information on the abundance, distribution, and movements of juvenile lake trout in 1958–63. Experimental fishing was done at several locations among the Apostle Islands and in Keweenaw Bay (Fig. 1). Experimental gill nets — each 300 ft (91m) long and 6 ft (1.8 m) deep, of 1–5-inch (25.4–127-mm) mesh by ½-inch (12.7-mm) intervals; and bottom trawls, 31-ft (9.4-m) semiballoon, of 2½-inch-mesh (63.5-mm) body, and ½-inch-mesh (12.7-mm) codend — were fished at various depths at each location. The gill nets usually were fished 1 night and the trawls towed 15 min. Total length (inches) was recorded for each fin-clipped fish. Of the lake trout captured in trawls, 102 fish taken at Frog Bay only a few hours after release were not included in the records of Table I. Observations in Keweenaw Bay were based on 431 fish taken in trawls.

Information on catches of fin-clipped lake trout from the Wisconsin commercial fishery was collected in 1959–62 by both the Wisconsin Conservation Department and the Bureau of Commercial Fisheries. Wisconsin personnel accompanied commercial fishermen and checked their catches until the season was closed on June 30, 1962. For the remainder of 1962 the Department used its own boat and employed fishermen to fish in the same manner as in previous

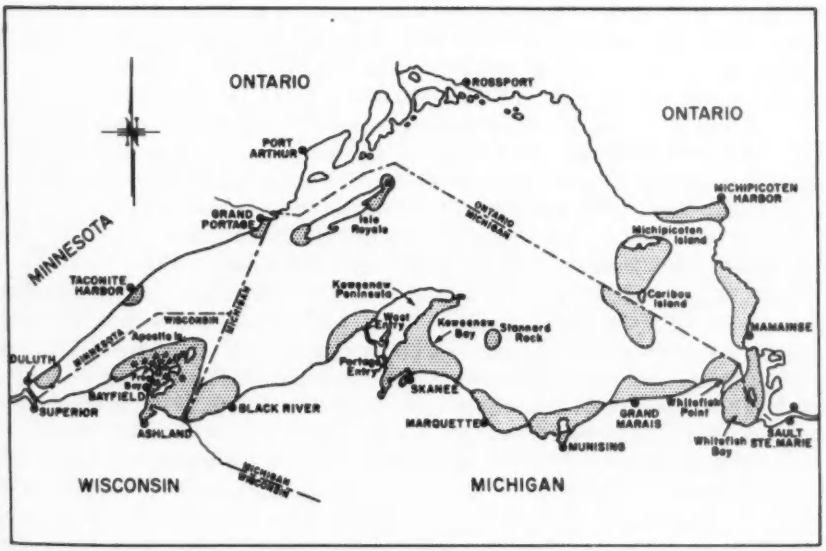

FIG. 1. Areas (stippled enclosures) of Lake Superior from which samples were obtained.

TABLE I. Number of hatchery-reared lake trout captured per hour of trawling according to time out and distance traveled (total numbers of fish captured are in parentheses; 1 mile = 1.609 km).

Months after planting	Distance from nearest planting site (*miles*)				
	<2	2–4	5–7	8–10	10–30
<3	19.6 (49)	2.8 (11)	4.7 (13)	1.6 (7)	0.0 (0)
3–4	32.5 (138)	49.4 (247)	5.5 (11)	2.3 (9)	0.6 (1)
5–7	16.0 (12)	29.9 (299)	7.2 (9)	4.0 (4)	1.3 (5)
12–14	9.0 (36)	25.3 (417)	7.8 (49)	9.1 (41)	3.3 (34)
15–16	3.7 (12)	32.7 (180)	10.8 (62)	6.3 (36)	1.1 (2)
17–18	12.0 (3)	14.0 (105)	4.0 (3)	6.0 (6)	2.3 (4)

years. The Bureau employed one Wisconsin commercial fisherman to keep complete records of his catch. This fisherman also fished off Black River in Michigan.

All data from Michigan waters were collected by the Bureau in 1959–63. In March 1959, nine of the most productive commercial fishermen in Michigan were employed to collect data from their own catches. Most of these fishermen have provided data regularly since that time. (A limited amount of fishing was allowed under contract to the Bureau after the season closure.)

Data from Ontario waters of eastern Lake Superior, available only for 1961 and 1963, were provided by the Fisheries Research Board of Canada, Biological Station, London, Ontario. Information was collected by both fishery technicians and commercial fishermen employed by the Board.

The Minnesota Department of Conservation provided data collected by commercial fishermen operating under special permits in 1963.

All agencies collected essentially the same information. Each fish caught was examined for clipped fins and lamprey wounds and scars. Scale samples and measurements were collected from entire catches or net-run samples according to schedules established by the agencies. All fin-clipped fish were measured. The amount of gear fished, location of the set, and number and total weight of fish caught were recorded for each lift.

In Wisconsin, 12.3–21.2% of the total commercial production of lake trout was sampled each year in 1959–62. The Bureau's samples comprised 27.9–47.9% of the total Michigan production in the same years. Since the closure of the lake trout season in mid 1962, all commercial production of lake trout in US waters has been monitored.

TABLE II. Average length (inches) of hatchery-reared lake trout in the Apostle Islands region, arranged according to distance traveled and time at liberty. (Number of fish in parentheses; 1 inch = 25.4 mm; 1 mile = 1.609 km.)

Months at liberty	Distance from nearest planting site (*miles*)				
	<2	2–4	5–7	8–10	10–30
12–14[a]	8.1 (8)	7.9 (278)	8.2 (30)	7.9 (8)	8.1 (23)
24–26[b]	... ...	11.6 (77)	... ...	11.7 (172)	... ...
36–38[c]	... ...	13.8 (76)	... ...	13.9 (111)	... ...

[a]Based on trawl catches of lake trout planted in 1962.
[b]Based on gill net catches of lake trout planted in 1961.
[c]Based on gill net catches of lake trout planted in 1960.

The areas from which data were collected (Fig. 1) included all important lake trout fishing grounds in US waters in 1959–63. Samples were well distributed throughout the areas. Most of the data used in this report came from the areas along the south shore. The number of fin-clipped fish caught in these areas was substantial and complete information on fishing effort was available. The other areas indicated in Fig. 1 provided more limited information because data were not available for an unbroken series of years, the catch of fin-clipped fish was low, or information on fishing effort was lacking.

Although fin-clipped lake trout were planted in Lake Superior every year in 1952–61 (except 1957), the materials in this report are limited, with two exceptions, to returns of fish from plantings that had distinctive marks not used elsewhere. Two marks were repeated in other areas, but were used for year-classes 4 and 6 years apart, and these fish could easily be distinguished by size alone. Summaries of returns from all plantings were made from data collected in 1959–62. Complete 1963 data available at the time of writing for four Michigan plantings were also included.

Returns of fin-clipped lake trout were assigned to given plants by one or more criteria. Nearly half the fish bore fin-clip combinations which were used only once and could not be confused with fish from other plantings, but those planted in the Apostle Islands in 1952–54, 1956, and 1958 all bore the same mark. Young fish bearing fin marks which were not used more often than once in 2 years could be identified from the fin mark and the length of the fish; but within 2 or 3 years after release the lengths of individuals from a plant were so variable that some could be identified only after ages were determined from scales. The ages of fish in a subsample of fin-clipped trout were applied by length groups to the samples of fish bearing the same mark to obtain estimates of the number recaptured from each planting. Fish recaptured from the 1952–54 plantings in the Apostle Islands, all of which bore the same fin mark, were

assigned arbitrarily to 1954; examinations of scales indicated insignificant numbers of returns from fish stocked in 1952 and 1953.

Ages were determined from plastic impressions of the scales of 1538 fish that bore the fin mark of those planted in the Apostle Islands prior to 1960. Impressions were made with a modified jewelers press (Smith, 1954), and were read at a magnification of 83× on a microprojector. Most scales of hatchery-reared lake trout could be read accurately, but age determinations were occasionally complicated by the frequent presence of two marks in close proximity, either one of which could have been the first annulus. Although it is possible the first mark was the "0-mark" described by Cable (1956), it is believed that more probably the second mark was an accessory check laid down at the time the fish was planted. Because the only groups for which age determinations were necessary were planted at 2-year intervals, the presence of an accessory mark caused little difficulty in assigning fish to their respective plantings.

Nearly all data used in this study came from catches of fish planted in the spring as yearlings. Returns from plantings of fall fingerlings in the Apostle Islands in 1952–53 were included in Table III and Fig. 2 but were not used elsewhere.

TABLE III. Location and number of recoveries of hatchery-reared lake trout planted in various areas of Lake Superior.

Area of capture	Area of planting					Total
	Apostle Islands	Keweenaw Bay	Marquette	Munising	Whitefish Bay	
South shore						
Apostle Islands	8,210	1	0	0	0	8,211
Black River	340	0	0	0	0	340
West Entry	1,366	13	0	0	0	1,379
Keweenaw Bay	1,117	3,282	990	108	14	5,511
Marquette	137	55	292	303	9	796
Munising	416	100	264	1,411	55	2,246
Grand Marais	186	5	20	315	301	827
Whitefish Point	19	3	5	2	71	100
Whitefish Bay	5	0	1	0	1,865	1,871
East shore						
Mamainse	14	0	8	0	150	172
North shore and offshore	47	0	1	0	52	100
Total:	11,857	3,459	1,581	2,139	2,517	21,553

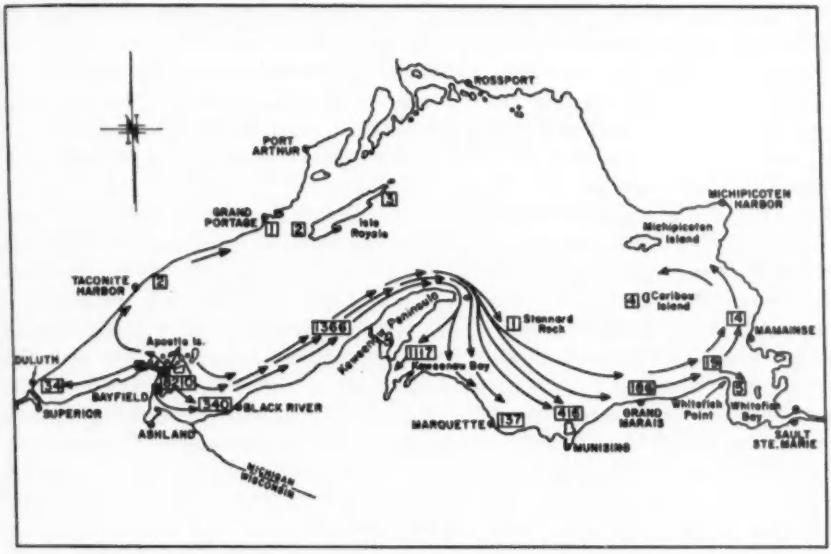

FIG. 2. Localities and number of returns of hatchery-reared lake trout planted in the Apostle Islands. Black squares are planting localities and open rectangles give the number of fish caught in each area; arrows indicate direction of movement.

The data on catch of fin-clipped fish per unit effort were based on lifts of approximately 50 million ft (15.2 million m) of 4½-inch-mesh (114-mm) gill nets (braided nylon material). The average length of a gang of gill nets in a lift was roughly 15,000 ft (4572 m).

The map of surface currents of Lake Superior (Fig. 7) is a modification of a chart published by Harrington (1895). The original has been changed somewhat, according to recent findings of the Bureau's Biological Laboratory at Ann Arbor, Michigan. Some of the laboratory's data were included in Beeton *et al.* (1959). Additional unpublished records were obtained from the laboratory files.

POSSIBLE SOURCES OF BIAS OR ERROR

Analyses based on records of catch per unit effort (CPE) of individual fishermen are susceptible to several possible sources of bias. Differences in efficiency of the fishermen in the various areas is the most obvious. The fishermen in operation on Lake Superior in 1959–62 were the survivors of economic attrition through most of the 1950s. As abundance of lake trout declined, only the efficient operators were able to continue fishing. The efficiency of fishermen whose catches were sampled undoubtedly varied somewhat, but differences were minimized by earlier attrition of the less efficient. The gear used by all fishermen was practically identical.

Differential movement of various size groups within a year-class of planted fish or differential growth rates resulting from movement to other areas could

bias the data strongly. The fish of any planting caught in areas away from the planting site were usually grouped closely around the modal size for the group in the area where the fish were planted. Both the largest and smallest fish of a year-class in any one year were usually caught in the area where they were planted. Bias due to differential movement of various size groups or to different growth rates in the various sampling areas appears to have been inconsequential.

Differential mortality of lake trout in various areas could affect apparent movement. The sea lamprey invaded Lake Superior from the east end and reduced abundance of lake trout in the eastern part of the lake earlier than in the western end. By 1957 or 1958, lamprey activity (estimated from catches of lampreys in spawning streams and from the incidence of wounds on lake trout) was roughly equal in all areas along the south shore. In 1962–63, the incidence of lamprey wounds declined in all areas, but the most drastic decline was in the western end of the lake. Differential mortality of lake trout due to lamprey predation would lead to underestimates of the extent of movement eastward from the Apostle Islands, but this bias probably applies only to the Apostle Islands plantings of 1952–54. Lake trout appeared to be immune to lamprey attack for the first 2 or 3 years after release.

The bulk of the fishing effort in most areas was exerted in the spring and fall, the times of the year when fishing success was highest. Fishing was done only in the spring, when fishing was best, at Black River and in Whitefish Bay. Much of the fishing off West Entry was in the summer and early fall, when fishing was poor. The data of Tables IV and V, therefore, are biased toward overly high values at Black River and Whitefish Bay and low values at West Entry.

The possibility of chance error for average CPE values varies with the amount of gear lifted and number of lifts. In 1959, the samples in each area except Black River were obtained from lifts of over 1,250,000 ft of gill net. Effort declined in all areas in each succeeding year. In 1962 only the Keweenaw Bay sample was based on more than 1 million ft of net; for Grand Marais, Whitefish Point, and Whitefish Bay the total was 200,000–315,000, and in all other areas except Black River, 625,000–981,000 ft. Effort in the Black River area declined from 253,000 ft in 1959 to only 42,000 ft in 1962. Although fishing effort was too low to yield reliable averages for this area in both 1961 and 1962, the CPE values for fin-clipped fish were very close to those from nearby Wisconsin waters near the Michigan border. CPE values from Black River for 1961–62 are included because they were entirely consistent with other data, but are, obviously, less reliable than those from other areas.

EARLIER MIGRATION STUDIES IN THE UPPER GREAT LAKES

The earliest large-scale, systematic study of lake trout movements in the upper Great Lakes was that of Smith and Van Oosten (1940), who tagged 1416 fish near Port Washington, Wisconsin, in Lake Michigan. These fish were 6–17 inches (152–432 mm) total length at tagging and averaged 12.8 inches

(325 mm). Of their 218 recaptures, 53% came within 1 year and 73% were within 25 miles (40 km) of the tagging site. It required 3 years for lake trout to become scattered throughout the lake. Most immature fish moved northward from the tagging site on the west-central shore and followed the shoreline. Mature fish were recaptured in all directions from the point of release. Four of the 218 fish had moved more than 125 miles (201 km).

Fry (1953) reported that nearly all tagged lake trout released in South Bay, Manitoulin Island (Lake Huron), remained within the bay. South Bay is connected to Lake Huron only through a shallow, 700-ft-wide (213-m) narrows.

Eschmeyer *et al.* (1953) reported on returns from 733 tagged native lake trout released in Lake Superior. Although only 25 mature fish were recaptured, the data suggested that large, mature fish tagged on spawning grounds near Keweenaw Point, Michigan, dispersed widely throughout the lake after the spawning season, but that most fish returned to the general vicinity of tagging in subsequent spawning seasons. Immature fish released just west of the Apostle Islands in Wisconsin were recovered (140 returns) in Wisconsin (76.4%), Minnesota (14.3%), and Michigan (9.3%). Although three fish had traveled at least 255 miles (410 km), 90% of the recoveries were within 50 miles (80 km) of the tagging locality.

Eschmeyer (1955) reported on 83 recaptures of mature lake trout tagged on spawning grounds near Marquette, Michigan. Of 33 fish returned in the 10-month intervals between spawning seasons, 25 were taken at distances of 14–198 miles (23–319 km) — average, 67 miles (108 km) — from the tagging site and eight were taken within 5 miles (8 km) of the tagging site. Five of these eight fish were taken within 1 month of the onset of the spawning season and might have been early arrivals on the grounds. Of 36 fish recaptured during subsequent spawning seasons, 27 were taken near the grounds where they were tagged, eight were taken near other spawning areas, and one was taken far from any known spawning ground. The remainder of the fish were recaptured within 26 days of tagging; 10 fish were on the grounds where tagged and four were on other spawning grounds 26–97 miles (42–156 km) from the tagging site. Because not all fish were actually spawning when tagged, some may have been en route to other spawning areas. The precise degree of "homing" could not, therefore, be determined.

Loftus (1958) reported that mature lake trout from river-spawning populations in eastern Lake Superior did not range widely. Most (96%) of the recoveries were within 30 miles (48 km) of the tagging site and only one fish was recaptured more than 70 miles (113 km) away. All stream recoveries were in the same streams where the fish were tagged, but nearby streams were not sampled until later years, after the stocks had been nearly exterminated.

TABLE IV. Number of lake trout from various plants caught per million ft (304,801 m) of commercial gill net lifted (CPE) in south and east sampling areas in each year of capture (dashes indicate no data).

Planting area, year(s), and age	Year captured	Area of capture								
		West of Keweenaw Peninsula			East of Keweenaw Peninsula					
		Apostle Islands	Black River	West Entry	Keweenaw Bay	Marquette	Munising	Grand Marais	Whitefish Point	Whitefish Bay
Apostle Islands										
	1959	160.5	169.9	49.7	8.1	2.2	14.0	26.8	...	...
1954	1960	47.0	54.1	5.6	10.1	0.0	8.4	23.8	...	...
(yearlings)	1961	0.0	0.0	0.7	14.3	2.7	8.1	10.8	5.4	0.0
	1962	0.0	0.0	1.4	2.2	0.0	0.0	0.0	0.0	0.0
	1959	258.5	118.5	128.3	4.6	1.3	8.2	15.4	...	...
1956	1960	570.9	576.6	269.3	26.8	1.1	22.2	59.5	...	...
(yearlings)	1961	683.0	954.4	254.0	94.2	29.9	78.7	68.6	27.2	2.8
	1962	660.1	856.8	130.4	88.3	68.7	107.1	79.6	27.4	9.5
	1959	26.7	4.0	0.0	0.1	0.0	0.4	0.0	...	...
1958	1960	38.0	63.1	4.2	0.9	4.4	1.1	4.0	...	...
(yearlings)	1961	267.6	151.5	120.8	7.5	2.7	8.1	3.6	0.0	0.0
	1962	812.2	357.0	148.0	40.0	44.7	117.9	84.6	23.5	3.2
	1959	3.1	0.0	0.0	0.0	0.0	0.0	0.0	...	...
1959	1960	9.8	0.0	1.3	0.0	0.0	0.0	0.0	...	...
(yearlings)	1961	40.8	45.5	10.2	2.9	0.0	0.0	1.8	0.0	0.0
	1962	805.0	71.4	146.7	9.8	12.8	24.1	14.9	0.0	0.0
	1960	1.6	0.0	0.0	0.0	0.0	0.0	0.0	...	...
1960	1961	64.2	45.5	0.7	0.0	0.0	0.0	0.0	0.0	0.0
(yearlings)	1962	381.6	95.2	19.0	1.5	0.0	2.4	0.0	0.0	0.0
Keweenaw Bay										
	1959	0.0	0.0	0.0	1.1	0.0	0.0	0.0	...	...
1959	1960	0.0	0.0	0.0	19.2	0.0	1.1	0.0	...	...
(2-year-olds)	1961	0.0	0.0	0.0	87.1	0.0	0.0	0.0	0.0	0.0
	1962	0.9	0.0	9.5	241.7	9.6	12.0	14.9	0.0	0.0
	1963	...	...	4.0	241.7	19.9	8.3	0.0	0.0	0.0
Keweenaw Bay										
	1960	0.0	0.0	0.0	0.0	0.0	0.0	0.0	...	...

Keweenaw Bay										
	1960	0.0	0.0	0.0	0.0	0.0	0.0	0.0	...	...
1960	1961	0.0	0.0	0.0	11.8	0.0	0.0	0.0	0.0	0.0
(yearlings)	1962	0.0	0.0	0.0	96.2	1.6	7.2	10.0	0.0	0.0
	1963	...	...	1.0	427.8	59.6	11.22	0.0	13.3	0.0
Marquette										
	1959	0.0	0.0	0.0	0.4	2.6	0.0	0.0	...	...
1958	1960	0.0	0.0	0.0	8.2	13.2	24.3	0.0	...	...
(yearlings)	1961	0.0	0.0	0.0	27.8	65.3	98.5	16.2	10.9	0.0
	1962	0.0	0.0	0.0	20.6	55.9	60.2	14.9	0.0	3.2
	1959	0.0	0.0	0.0	3.0	1.3	0.0	0.0	...	...
1959	1960	0.0	0.0	0.0	36.3	0.0	7.4	0.0	...	...
(2-year-olds)	1961	0.0	0.0	0.0	56.4	61.7	1.8	0.0	0.0	0.0
	1962	0.0	0.0	0.0	110.7	116.6	49.4	10.0	0.0	0.0
	1959	0.0	0.0	0.0	0.4	0.0	0.0	0.0	...	...
1959	1960	0.0	0.0	0.0	24.1	7.7	14.8	0.0	...	...
(3-year-olds)	1961	0.0	0.0	0.0	18.6	6.4	5.4	9.0	0.0	0.0
	1962	0.0	0.0	0.0	6.8	14.4	14.4	5.0	11.8	0.0
Munising										
	1960	0.0	0.0	0.0	0.0	0.0	0.0	0.0	...	...
1960	1961	0.0	0.0	0.0	0.0	0.0	6.3	16.3	0.0	0.0
(yearlings)	1962	0.0	0.0	0.0	7.1	24.0	387.7	44.8	0.0	0.0
	1963	...	...	0.0	38.3	520.3	1,785.5	593.5	8.9	0.0
Whitefish Bay										
	1961	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
1961	1962	0.0	0.0	0.0	0.6	0.0	15.7	5.0	0.0	3.2
(yearlings)	1963[a]	...	...	0.0	5.4	16.3	69.3	599.5	315.6	2,002.1

[a]CPE at Mamainse, Ontario, was 146.1.

TABLE V. Number of lake trout from various planting sites caught per million of feet of commercial gill net lifted (CPE) in each sampling area for each year at large, expressed as a percentage of the sum of the CPE values for all areas for each year at large (dashes indicate no data).

Planting area, year(s), and age	Years[a] at large	Area of capture									Total number of returns
		West of Keweenaw Peninsula			East of Keweenaw Peninsula						
		Apostle Islands	Black River	West Entry	Keweenaw Bay	Marquette	Munising	Grand Marais	Whitefish Point	Whitefish Bay	
Apostle Islands											
	1	100.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	12
1954	2	77.4	18.0	4.1	0.1	0.0	0.4	0.0	0.0	0.0	234
1956	3	49.8	39.5	5.8	1.3	1.3	0.5	1.8	0.0	0.0	677
1958–60	4	50.2	26.8	18.5	1.0	0.5	1.5	1.5	0.0	0.0	2,784
(yearlings)	5	43.2	29.5	13.3	2.2	1.4	4.3	4.5	1.4	0.2	3,098
	6	33.9	41.2	11.5	3.1	1.0	3.4	4.6	1.2	0.1	2,911
	7	31.6	39.0	5.0	5.5	1.7	5.4	9.9	1.4	0.5	1,491
	8	0.0	0.0	1.7	34.0	6.4	19.3	25.7	12.9	0.0	60
	9	0.0	0.0	38.9	61.1	0.0	0.0	0.0	0.0	0.0	8
Keweenaw Bay											
	1	0.0	0.0	0.0	100.0	0.0	0.0	0.0	...	...	8
1959	2	0.0	0.0	0.0	94.6	0.0	5.4	0.0	...	...	64
(2-year-olds)	3	0.0	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0	244
	4	0.3	0.0	3.3	83.7	3.3	4.2	5.2	0.0	0.0	813
	5	...	...	1.5	88.2	7.3	3.0	0.0	0.0	0.0	555
	1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0
1960	2	0.0	0.0	0.0	100.0	0.0	0.0	0.0	0.0	0.0	33
(yearlings)	3	0.0	0.0	0.0	83.6	1.4	6.3	8.7	0.0	0.0	325
	4	...	...	0.2	69.7	9.7	18.3	0.0	2.1	0.0	1,053
Marquette											
	1	...	...	...	...	...	...	...	...	...	...
1958	2	0.0	0.0	0.0	13.3	86.7	0.0	0.0	...	...	9
(yearlings)	3	0.0	0.0	0.0	17.9	28.9	53.2	0.0	...	...	62
	4	0.0	0.0	0.0	12.7	29.9	45.0	7.4	5.0	0.0	270
	5	0.0	0.0	0.0	13.3	36.1	38.9	9.6	0.0	2.1	156

Marquette											
	1	0.0	0.0	0.0	69.8	30.2	0.0	0.0	...	...	25
1959	2	0.0	0.0	0.0	83.1	0.0	16.9	0.0	...	...	126
(2-year-olds)	3	0.0	0.0	0.0	47.0	51.5	1.5	0.0	0.0	0.0	228
	4	0.0	0.0	0.0	38.6	40.7	17.2	3.5	0.0	0.0	476
	1	0.0	0.0	0.0	100.0	0.0	0.0	0.0	...	...	3
1959	2	0.0	0.0	0.0	51.7	16.5	31.8	0.0	...	...	100
(3-year-olds)	3	0.0	0.0	0.0	47.2	16.3	13.7	22.8	0.0	0.0	70
	4	0.0	0.0	0.0	13.0	27.5	27.5	9.5	22.5	0.0	47
Munising											
	1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	...	...	0
1960	2	0.0	0.0	0.0	0.0	0.0	28.0	72.0	0.0	0.0	16
(yearlings)	3	0.0	0.0	0.0	1.5	5.2	83.6	9.7	0.0	0.0	369
	4	...	...	0.0	1.3	17.7	60.6	20.1	0.3	0.0	1,754
Whitefish Bay											
	1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0
1961	2	0.0	0.0	0.0	2.4	0.0	64.1	20.4	0.0	13.1	17
(yearlings)	3[b]	...	...	0.0	0.2	0.5	2.2	19.0	10.0	63.5	2,396

[a]The first year at large includes only the period from planting (April–June) until December 31. Other years are full calendar years.
[b]Value at Mamainse, Ontario, was 4.6.

MOVEMENTS OF LAKE TROUT RECAPTURED IN EXPERIMENTAL GEAR

Immediate Dispersal of Lake Trout Planted from Shore

To determine the time required for shore-planted lake trout to find suitable habitat and begin feeding, the M/V *Siscowet* made a series of trawl tows just offshore while lake trout were being planted from the beach at Frog Bay, Wisconsin (Fig. 1). Yearling fish (22/lb; 49/kg), planted in the spring of 1961, were captured at 5 fath (9 m) about 40 min after planting, at 10 fath (18 m) in 2½ hr, and at 15 fath (27 m) in 3½ hr. The depth of 15 fath, about 1 mile (1.6 km) from shore, was considered suitable habitat because both native and previously planted lake trout were abundant there. The experiment was repeated in the spring of 1962 with similar results. Another experiment with older fish in the fall of 1962 revealed that fall-planted 20-month-old lake trout dispersed faster than did spring-planted yearlings. The larger fall-planted fish (8/lb; 18/kg) reached 10 fathoms in about 1 hr, 1½ hr sooner than the spring-planted fish.

Stomachs were examined from lake trout planted in the spring of 1961 at 6, 24, and 48 hr after planting. The first evidence of feeding was obtained 48 hr after planting.

Dispersal Through the First Three Years of Liberty

The records of hatchery-reared lake trout captured in trawls in 1961–62 (Table I) offer a general idea of dispersal after planting at shore. Most of the lake trout were found in waters less than 2 miles (3.2 km) from the nearest planting site during the first 2 months after planting. The number of fin-clipped lake trout captured per hour of trawling decreased from 19.6 at less than 2 miles to 1.6 at 8–10 miles (13–16 km) from the planting site. No fish was taken at distances greater than 10 miles (16 km) during the first 2 months. In 3–4 months after release, the planted lake trout were most abundant (49.4 fish per hour of trawling) at 2–4 miles (3.2–6.4 km), and one fish was taken at 17 miles (27 km). Between 5 and 14 months after planting, the abundance of planted fish generally increased at distances greater than 4 miles and decreased at distances less than 4 miles from the planting site. Despite the apparent relation between time out and distance traveled, the fish were most abundant at 2–4 miles up to 18 months after planting. Catches in experimental gill nets supported the findings from trawl catches. Fish planted at Bayfield in 1960 were still most abundant at 2–4 miles from the planting site after 3 years at large.

The general decline in catch per unit effort of trawls in all areas after 14 months was probably due to the increased size of the fish and the more general dispersal to outlying waters. As the fish grew larger they became less vulnerable to the trawl. Lake trout more than 15 inches (381 mm) long were rarely taken in experimental trawls. As the fish spread to outlying waters, they obviously became relatively less abundant in areas adjacent to the planting site.

Little correlation was apparent between the average size of the lake trout and the rate of dispersal from the planting site. Catches made in trawls and experimental gill nets in 1963 provided comparisons among the average lengths of hatchery-reared lake trout taken at various distances and lengths of time at large (Table II). The average length of lake trout captured less than 2 miles (3.2 km) from the planting site (8.1 inches; 206 mm) was the same as that for fish caught more than 10 miles (16 km) away. The average lengths of fish at large 2–3 years were also nearly the same regardless of the distance traveled.

Fishing by the *Siscowet* was less intensive in Michigan waters of Lake Superior than in the Apostle Islands region, but yielded similar results. Fish which had been planted in lower Keweenaw Bay (Fig. 1) were most abundant 2–4 miles (3.2–6.4 km) from the planting site up to 3 years after planting. The abundance of hatchery-reared lake trout decreased progressively with distance from the planting site.

MOVEMENTS OF PLANTED LAKE TROUT CAUGHT IN COMMERCIAL GEAR

The total returns, in various sampling areas, of marked fish planted in a single area are sufficient to show where fish move. Variations in fishing intensity and sampling and the rates of movement and survival determine how many fish actually are recovered in the different areas. A measure of relative abundance of marked fish that is comparable in all sampling areas is needed, therefore, to show what proportion of the fish leave the area in which they were planted. The only measure of relative abundance that is reasonably dependable for comparisons among all sampling areas is the number of marked fish caught per unit effort. After release, lake trout become progressively more vulnerable to the commercial fishing gear, but do not reach a size that makes them fully vulnerable (roughly 20 inches long; 508 mm) for several years. Variation in growth of lake trout is so great that some individuals may reach 20 inches in the 3rd year after planting, but others do not attain this length until the 6th or 7th year. Comparisons of CPE values among the sampling areas are, therefore, valid only for fish from a given planting that have been at liberty the same number of years.

If CPE values for all areas in which fish from a given planting were caught are summed for a particular year of collection, CPE in any area can be expressed as a percentage of this sum. The "area percentage" or "percentage CPE" values are estimates of the relative abundance in each area of the surviving fish from a plant in the year considered. These percentages are comparable for different years of collection. If, for example, fish from a plant made in the Apostle Islands yield a CPE of 10 in the Apostle Islands area and 0 in all other sampling areas during the first year at large, the percentage CPE value in the Apostle Islands is 100. The following year this group of fish might yield a CPE of 40 in the Apostle Islands, 10 in the Black River area, and 0 in all

other areas. The CPE values are not comparable to those of the previous year because of the effects of mortality and of increased vulnerability to the gear through growth, but the percentage CPE values of 80 in the Apostle Islands and 20 at Black River are comparable. During the 1st year, all fish were still in the Apostle Islands area, but in the 2nd year they were one-fourth as abundant at Black River as in the Apostle Islands. In this example, substantial movement from the Apostle Islands to the Black River area would be indicated.

The information on returns of fin-clipped lake trout is presented in three forms. The total numbers of returns in the various areas from plants made in given areas (Table III, Fig. 2–6) show the locations of all returns and the directions of movement. The annual CPE values by area for various plants (Table IV) show the differences in catch rates (CPE values are computed only for major south shore sampling areas). Percentage CPE values computed by the method described above show the relative abundance of fish planted in various locations in each area (Table V). The percentages were listed by years at large; those for plants in the Apostle Islands, where all fish stocked were yearlings, are averages for several plants.

Lake Trout Planted in the Apostle Islands

Lake trout planted in the Apostle Islands were caught in every area sampled in US waters and in Ontario waters at the east end of the lake (Table III, Fig. 2). The bulk of the returns (8210) came from the Apostle Islands, but substantial numbers were taken in Michigan waters to the east. Most of the movement appears to have been along the shoreline through the waters off Black River (340 returns) and West Entry (1366 returns) into areas east of the Keweenaw Peninsula. Keweenaw Bay had 1117 returns but Marquette had only 137. Returns from both Munising (416) and Grand Marais (186) were greater than those from Marquette. Eastward movement continued into waters north of Whitefish Point (19 returns), but only five fish from the Apostle Islands were caught in Whitefish Bay. Apparently, the fish turned northward from Whitefish Point and entered Ontario waters (14 returns in 1961; no data for other years) along the east shore. The 34 returns from Minnesota waters at the extreme western end of the lake indicate some dispersal westward. The small number of returns (three) from other Minnesota waters indicates only limited movement northeastward along the Minnesota shore. The small numbers of returns from Isle Royale (five), Stannard Rock (one), and Caribou Island (four) suggest little movement to these offshore waters.

Although the total numbers of returns give the distinct impression that most lake trout planted in the Apostle Islands remained in the area, the CPE values (Table IV) indicate a substantial amount of movement. The CPE in areas east of the Apostle Islands increased progressively from west to east after the fish were released. The CPE for some plants was as high off Black River as in the Apostle Islands by the 3rd year at large. The relation of abundance in the various areas to length of time the fish were in the lake is illus-

trated better by the percentage CPE values (Table V). During the 1st year at large, returns came only from the Apostle Islands (percentage CPE, 100). In the 2nd year at large some fish were caught off Black River (percentage CPE, 18.0) and off West Entry (percentage CPE, 4.1) and a very few were caught east of the Keweenaw Peninsula. By the 4th year, the percentage CPE in the Apostle Islands had declined to 50.2 and had increased to 18.5 at West Entry, but was still low or nil east of the Keweenaw Peninsula. In the 5th year, the fish reached Whitefish Point and Whitefish Bay in the eastern part of the lake and the percentage CPE increased substantially in the areas from Keweenaw Bay east through Grand Marais. The percentage CPE continued to decline in the Apostle Islands, increased at Black River, and began to decline at West Entry. By the 7th year at large, percentage CPE had decreased to 31.6 in the Apostle Islands, was higher at Black River than in the Islands, and was over 5.0 in three areas east of the Keweenaw Peninsula. In the 8th and 9th years all returns came from outside the Apostle Islands region, but the total number of returns was small.

Marquette consistently had a lower percentage CPE than Keweenaw Bay, Munising, and Grand Marais, and had a lower value than Whitefish Point in some years. Fish from the Apostle Islands appear to bypass Marquette to some extent — perhaps by moving across deep water from the tip of the Keweenaw Peninsula to Munising and Grand Marais. Whitefish Bay had a very low value in all years. Although no CPE data were available from Ontario waters in 1959–62, the catch of 14 fish at Mamainse in 1961, a year of near collapse of fishing in Ontario, suggests strongly that fish from the Apostle Islands pass by Whitefish Bay and move northward into Ontario waters.

Lake Trout Planted in Keweenaw Bay

The available data for Keweenaw Bay cover two plantings and include returns in 1963. A planting of 2-year-old fish was made in 1959, and yearlings were stocked in 1960. Most of the returns (3282) came from Keweenaw Bay (Table III, Fig. 3). Principal movement out of the area was eastward, but only Marquette (55 captures) and Munising (100 captures) had enough returns to show significant movement. West Entry had 13 returns and the Apostle Islands had one return, the only evidence of limited dispersal westward.

The abundance data (Tables IV and V) suggest that the yearling fish of the 1960 plant dispersed more widely than did the 2-year-old fish planted in 1959. Fish from the 1959 planting tended strongly to remain near the planting site. In 2 of the 5 years at large, the percentage CPE in Keweenaw Bay was 100 and in the 5th year it was still 88.2. No fish from this planting moved as far east as Whitefish Point and few moved as far as Grand Marais. Fish from this plant were taken at West Entry in both the 4th and 5th years of liberty, but the percentage CPE was low in both years.

Dispersal of the 1960 plant was more strongly eastward. Although the percentage CPE in Keweenaw Bay was 100 in the 2nd year at large, it declined

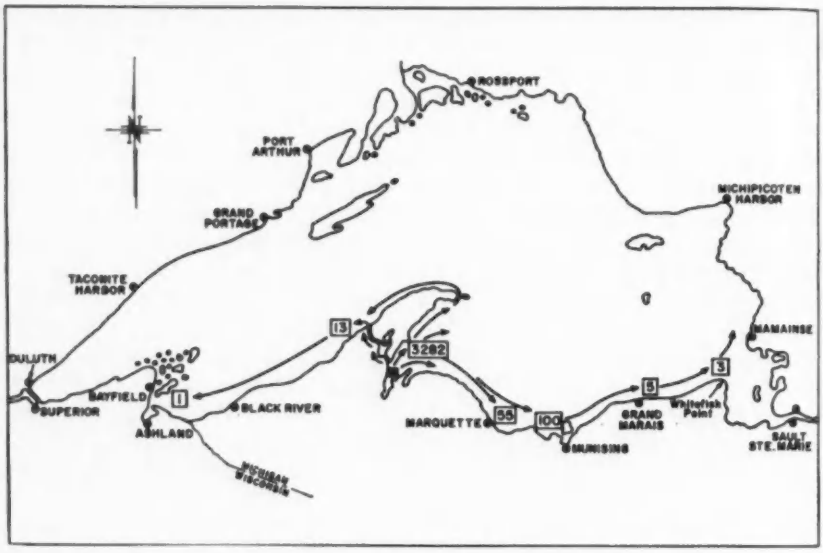

FIG. 3. Localities and number of returns of hatchery-reared lake trout planted in Keweenaw Bay. Black squares are planting localities and open rectangles give the number of fish caught in each area; arrows indicate direction of movement.

to 69.7 in the 4th year. A few fish from the plant reached Whitefish Point, but most of the movement was into waters near Marquette and Munising. Only one fish from the 1960 plant was taken at West Entry.

The fish that moved westward from Keweenaw Bay to West Entry and the Apostle Islands could have traveled either through the Keweenaw Waterway, a deep-water channel across the peninsula, or around the tip of the peninsula. The Keweenaw Bay entrance to the waterway lies within 7–8 miles (11.3–12.9 km) of the planting sites, and the waterway is only about 25 miles (40 km) long. The fact that no fish from these plantings were caught at West Entry until the 4th year at large suggests that some may have taken the longer route around the peninsula.

LAKE TROUT PLANTED OFF MARQUETTE

Yearling lake trout were planted off Marquette in 1958 and plantings of 2- and 3-year-old fish were made in 1959 (Tables III–V; Fig. 4). The older fish, as in Keweenaw Bay, dispersed differently from the yearlings. The total returns from all plants off Marquette suggest a strong westward movement into Keweenaw Bay (990 returns in the Bay and 292 off Marquette), but the abundance data show that the total returns are to a degree misleading.

Returns from the 1958 planting during the 2nd year at large (1959) indicated a significant movement into Keweenaw Bay (percentage CPE, 13.3) but most of the returns came from Marquette (percentage CPE, 86.7). Per-

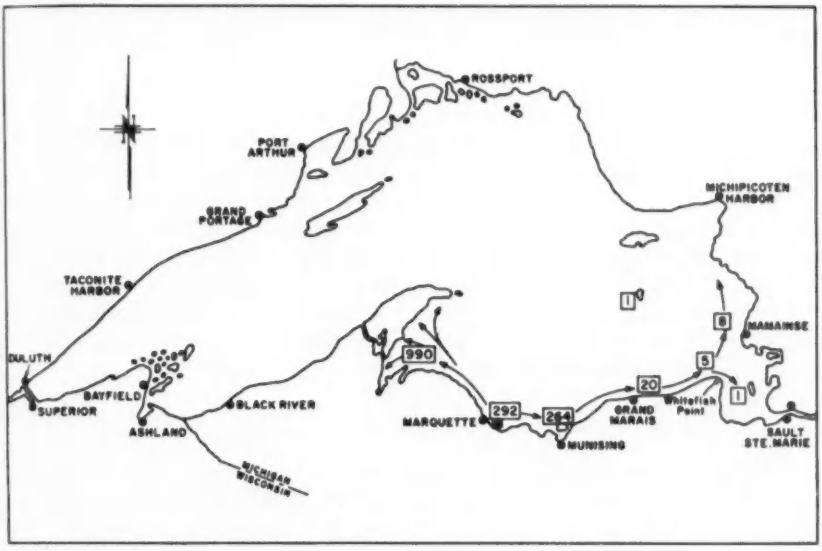

FIG. 4. Localities and number of returns of hatchery-reared lake trout planted off Marquette, Michigan. Black squares are planting localities and open rectangles give the number of fish caught in each area; arrows indicate direction of movement.

centage CPE increased little in the Bay after the 2nd year, but it declined at Marquette and increased progressively east of the planting site. Most of the movement from this plant was eastward.

Fish from the two 1959 plants were caught principally in Keweenaw Bay during the 1st year at large (percentage CPE values were 69.8 and 100). During the 2nd year, most of the fish planted as 2-year-olds were still caught in Keweenaw Bay (percentage CPE rose from 69.8 to 83.1) but the figure for those planted as 3-year-olds declined to 51.7. After the 2nd year, the percentage CPE for both groups declined in Keweenaw Bay and increased progressively from Marquette to Whitefish Point.

The early increase and later decline of the percentage CPE in Keweenaw Bay for the groups planted in 1959 suggest that most of the westward movement from Marquette to the Bay took place in 1959 and that most of the movement after 1959 was eastward. The almost constant percentage CPE in Keweenaw Bay for the 1958 fish suggests that much of the westward movement of this plant also took place in 1959. Some unusual condition seems to have existed in 1959; predominantly eastward movement could be expected for fish planted at Marquette in most years.

Only one fish from any of these plants was caught in Whitefish Bay, but five were taken north of Whitefish Point and eight were caught in Ontario in 1961 (data available for that year only). Fish from Marquette as well as those from the Apostle Islands appear to bypass Whitefish Bay. Only one

fish from these plants was taken in offshore waters and none was caught west of the Keweenaw Peninsula.

Lake Trout Planted off Munising

Yearling lake trout were planted at Munising in 1960 (Tables III–V; Fig. 5). Fish from this planting were caught in all areas from Keweenaw Bay to Whitefish Point, but most of the returns were from Marquette to Grand Marais. Movements show little trend other than a random dispersal both eastward and westward along the shore. In the 3rd year at large, the percentage CPE was still 83.6 at Munising. In the 4th year, the percentage CPE declined to 60.6 at Munising and rose to 17.7 at Marquette and 20.1 at Grand Marais. No fish from this planting was caught in Whitefish Bay, offshore waters, or waters west of the Keweenaw Peninsula.

Lake Trout Planted in Whitefish Bay

A plant of yearling lake trout was made at the north end of Whitefish Bay only 1 mile (1.6 km) from the tip of Whitefish Point in 1961 (Fig. 6). Although the fish had been out only 3 years, the number of returns and CPE were large in 1963 (Tables III and IV). Data on both the number of returns and fishing effort were available from the Mamainse area in Ontario for 1963 and additional returns from unspecified gear were reported from both inshore

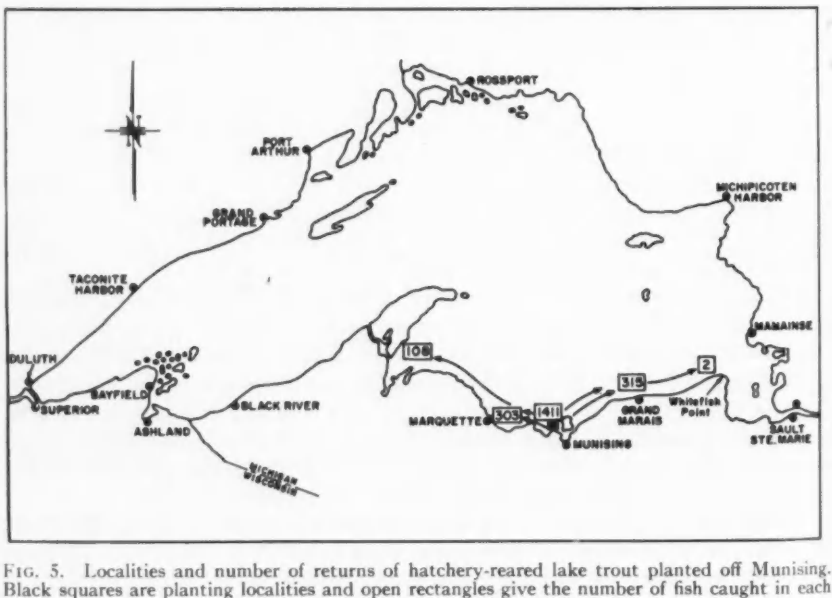

FIG. 5. Localities and number of returns of hatchery-reared lake trout planted off Munising. Black squares are planting localities and open rectangles give the number of fish caught in each area; arrows indicate direction of movement.

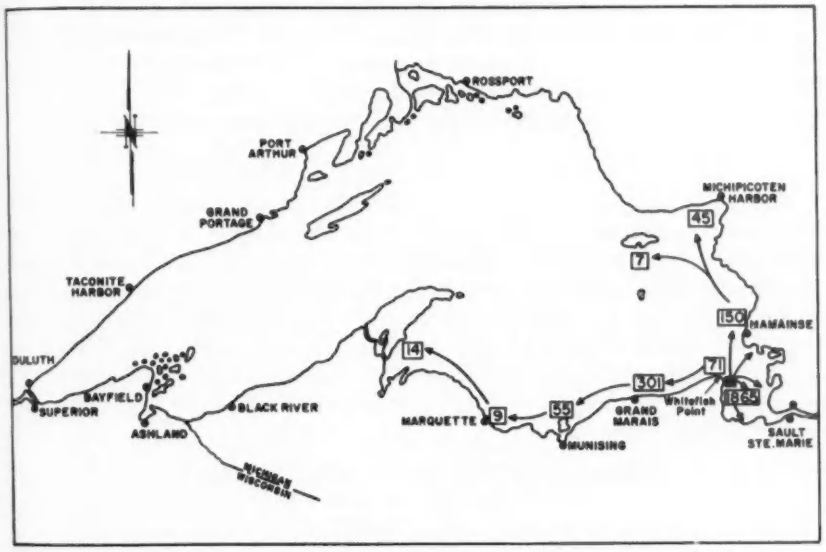

FIG. 6. Localities and number of returns of hatchery-reared lake trout planted in Whitefish Bay. Black squares are planting localities and open rectangles give the number of fish caught in each area; arrows indicate direction of movement.

and offshore waters (Michipicoten Harbor and Michipicoten Island), north of the Mamainse area for that year. The greatest number of fish was taken in Whitefish Bay, but many had moved into other areas. Returns came from every inshore area east of the Keweenaw Peninsula, and from all areas sampled in eastern waters of Ontario.

During the 3rd year at large, the percentage CPE was 63.5 in Whitefish Bay, 19.0 at Grand Marais, 10.0 north of Whitefish Point, and 4.6 in the Mamainse, Ontario, area (Table V). The relatively low percentage CPE off Whitefish Point as compared to Grand Marais is probably the result of sampling procedure. Samples were obtained from Whitefish Point only in the spring, but in both spring and fall at Grand Marais. The CPE values (Table IV) show that the vulnerability of these fish was increasing rapidly. Areas fished in the fall, therefore, had much higher CPE values than areas fished the previous spring. In the spring of 1963, the CPE was higher at Whitefish Point than at Grand Marais.

Although abundance of fish from this plant was highest by far in Whitefish Bay, many moved into the area north of Whitefish Point or into Ontario waters and dispersed westward or northward from there. The greatest movement was westward, but the percentage CPE was low west of Grand Marais. Movement northward to the Mamainse area was not great in view of its close proximity to the planting site. Although the Ontario returns from north of

the Mamainse area came from unspecified gear (which included some experimental trawls and small-mesh gill nets in addition to large-mesh commercial gill nets), the seven returns from the area south of Michipicoten Island indicate a greater offshore movement than from any single planting made in US waters. No fish from this planting was caught west of the Keweenaw Peninsula.

LAKE TROUT PLANTED IN CANADIAN WATERS

Although roughly ½ million yearling lake trout have been planted in Ontario waters annually since the spring of 1958, returns of these fish in US waters have been few. The total number of returns of Canadian fish in all samples was 40 as compared to roughly 30,000 (including some fish not part of the materials of this report) for fish planted in US waters. Although Isle Royale lies within 20 miles (32 km) of the site of one of the Canadian plantings, only one Canadian fish has been taken there. Canadian hatchery-reared lake trout have obviously made no important contribution to the populations in US waters.

THE RELATION BETWEEN SURFACE CURRENTS AND MOVEMENTS OF LAKE TROUT

Unless influenced by some strong external force, lake trout would be expected to disperse gradually in all possible directions from a planting site. Movements of planted lake trout in Lake Superior obviously have not been random. Fish stocked in the Apostle Islands region moved almost exclusively eastward to Michigan and Ontario waters, but the only movement from plantings east of the Keweenaw Peninsula to areas west of the peninsula was from plantings in Keweenaw Bay, and the number that moved was small. Fish planted in Keweenaw Bay tended strongly to remain in the area, and those that left the Bay generally moved eastward. Lake trout planted off Marquette moved generally eastward except in 1959. Fish planted in all areas outside Whitefish Bay bypassed that bay almost completely. A factor in this diversion may have been the shallow area that extends northward into the lake proper just to the west of Whitefish Point. Movement to offshore areas was low or nil from all plants. Only fish planted at Munising and in northern Whitefish Bay moved roughly at random along the shore. A comparison of movements of planted lake trout and of surface currents of Lake Superior suggests that currents are a principal factor influencing movements.

Lake trout usually are found at depths less than 50 fath (91 m) — most fishing is done at 10–45 fath (18–82 m) — and the 50-fath contour is less than 10 miles (16 km) from shore over most of southern Lake Superior. Hence, concentrations of lake trout are limited by depth to the areas along the shoreline.

The surface currents[3] (Fig. 7) in Lake Superior are generally counterclockwise and are much stronger along the south shore than along the north

[3]Although current studies in Lake Superior have all been done with floating bottles or cards, fishermen along the south shore have indicated that the currents extend to depths of about 45 fath during periods of high winds.

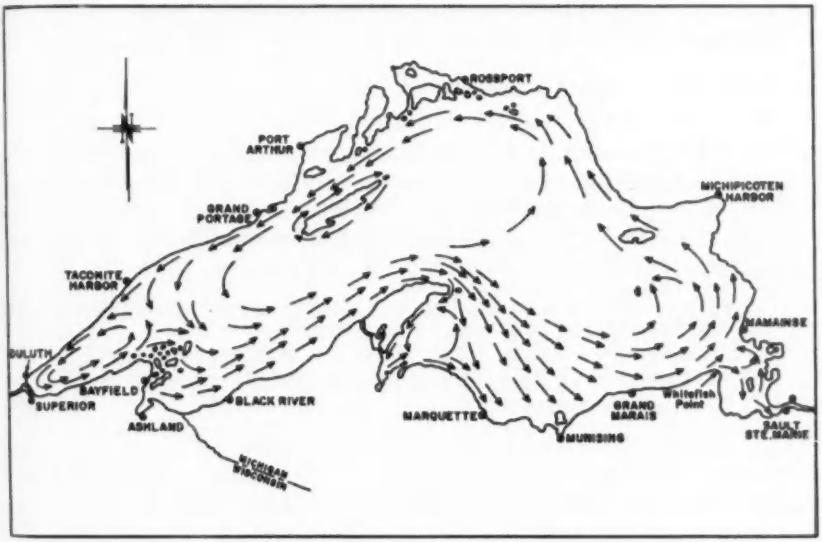

FIG. 7. Surface currents of Lake Superior.

shore. Large eddies exist in the extreme western end of the lake and in Keweenaw Bay. Whitefish Bay has only a weak counterclockwise flow. The currents are generated primarily by the prevailing westerly winds and are occasionally broken up by heavy winds from the east or northeast.

Similarities between the current flow and movements of lake trout (compare Fig. 2–4 with Fig. 7) indicate that lake trout move with the currents. If currents are responsible for the movements, areas with eddies or weak currents should show limited and random movement of lake trout. Lake trout planted in Keweenaw Bay tended to remain in the area. No fish have been planted in the eddy at the western end of the lake, but Eschmeyer *et al.* (1953) released tagged native lake trout on the Wisconsin shore in this area. About 90% of their recoveries were in Wisconsin waters or Minnesota waters west or northwest of the release point. Only one fish was caught in Minnesota northeast of the area covered by the eddy. Only 9.3% of the recoveries were in Michigan waters and these fish showed movements similar to those of hatchery-reared fish planted in the Apostle Islands. Although the data of Eschmeyer *et al.* (1953) are not strictly comparable to those from hatchery-reared fish, they indicate that lake trout within the eddy at the west end of the lake tend to remain there and that those that do move follow the current.

The evidence that currents exert a major influence on lake trout movements is summarized as follows:

1. Most of the movement of fish from the Apostle Islands followed the strong south-shore current eastward. Although a few fish moved westward into

the eddy at the west end of the lake, very few hatchery-reared or native fish moved up the Minnesota shore against the current.

2. Movement of fish from regions of eddies was far less than in areas of strong currents.

3. Movement to areas west of the Keweenaw Peninsula was insignificant from plants made in Keweenaw Bay and nil from other plantings farther east. (It is possible that fish stocked in the south end of Keweenaw Bay reached waters to the west through the Keweenaw Waterway and that none rounded Keweenaw Point.)

4. Movement from Keweenaw Bay and Marquette was mainly eastward with the current except in 1959.

5. The greatest amount of movement to an offshore area (from Whitefish Bay to Michipicoten Island) followed the main current.

6. Movement of lake trout from the bays and islands of the Ontario north shore to US waters has been insignificant. Currents are weak in this region. Movement from Ontario waters of extreme eastern Lake Superior against the current to US waters has also been negligible.

The lack of any strong trend in movements of fish planted at Munising and the predominantly westward movement of fish from the 1961 plant that moved out of northern Whitefish Bay are exceptions to the general statements on the effects of surface currents on lake trout movements. Currents in the eastern part of Lake Superior may be too weak, too variable, or too far offshore to have much influence on movements of fish planted in these areas. Recoveries of drift bottles released east of Grand Marais and north of Whitefish Point have shown that the eastward flowing current within about 4 miles (6.4 km) of shore is indeed weak. The stronger current 4–10 miles (6.4–16.1 km) offshore north of Whitefish Point moves northeastward into Ontario waters. More detailed knowledge of currents than is presently available is necessary for better understanding the relation with movements of lake trout in the eastern part of the lake. Although fish from all plantings show some tendency to disperse at random from a planting site, the relation between surface currents and major movements of lake trout seems to be strong.

SUMMARY OF MOVEMENTS OF LAKE TROUT

The proportion of planted lake trout that moves out of the general area of a planting site depends on the locality where the fish are planted and increases with the length of time the fish are at large. Dispersal from a planting site begins immediately after the fish are planted and probably continues until the fish are mature. Evidence that mature native lake trout disperse widely but return to the same grounds to spawn each year suggests that movements of mature fish may be entirely different from those of immature ones.

Fish from all plants in their dispersal from the planting site appeared not to go deeper than about 50 fath (91 m) offshore. Lake currents exerted an influence on dispersal and, in general, movement of lake trout was with the current. Fish planted in areas of strong currents dispersed more rapidly than those planted in regions of weak currents or eddies.

Whether lake trout are planted from boats within a few miles of shore or from shore should have little effect on the rate of dispersal to other areas. Lake trout planted from shore reach habitat occupied by both native and boat-planted fish within a few hours after planting.

Neither shore- nor boat-planting in inshore waters is effective for stocking offshore areas.

Where hatchery-reared lake trout will spawn remains to be determined. If lake trout should exhibit a true "homing" behavior and return to planting sites to spawn, present planting practices may have to be altered.

ACKNOWLEDGMENTS

Several people helped obtain materials for this study. A.H. Lawrie, Fisheries Research Board of Canada, Biological Station, London, Ontario, provided data requested on 1961 and 1963 returns of fin-clipped lake trout in eastern Ontario waters. C.R. Burrows, Minnesota Department of Conservation, St. Paul, Minnesota, provided 1963 data for Minnesota waters. Several commercial fishermen on Keweenaw Bay and at Marquette, Michigan, voluntarily provided information on their catches of lake trout in 1959 and 1960. Alfred M. Beeton, Bureau of Commercial Fisheries, Ann Arbor, Michigan, provided unpublished material on surface currents and advised in the preparation of Fig. 7. Ralph Hile read the manuscript and offered suggestions for presentation of the material.

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Time-Lapse Photography of an ASDIC Echo-Sounder PPI-Scope as a Technique for Recording Fish Movements During Migration[1,2]

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ABSTRACT

The use of time-lapse photography in combination with sonar as a means of observing the sockeye salmon (*Oncorhynchus nerka*) smolt migration in a large lake is discussed. A description of the gear used is given with some examples of the type of information that can be derived from this technique.

The scanning rate of the sonar equipment used, combined with time-lapse photography, resulted in a compression of time to $\frac{1}{288}$ when scanning at a range of 400 ft and to $\frac{1}{576}$ at a range of 800 ft. A 24-hr period may thus be viewed on film in respectively 5 and 2½ min when projected at a speed of 24 frames/sec. This speeded-up process facilitates separation of moving targets from stationary ones, even in the clutter of surface and/or ground echoes.

Although subject to all the usual vagaries of target identification which accompany use of all echo-sounding gear, analysis of the movies with a time-motion projector appears to give meaningful information on such parameters as the speed and direction of migration or movement, and the distribution of migratory activity throughout a 24-hr period.

INTRODUCTION

Water as a medium presents a number of problems in the study of behaviour of fishes in their natural environment. Except during daylight hours in extremely transparent waters and in very shallow depths, the scientist is groping in an unseen animal world.

One of the most promising developments for the detection of fish in recent years is that of echo-sounding and ranging (Kristjonsson, 1959, pp. 474–527). In this paper a technique will be discussed whereby time-lapse photography of the Plan Position Indicator scope (PPI scope) of an ASDIC sonar permits continuous observation of the migration of juvenile sockeye salmon (*Oncorhynchus nerka*). Basically this technique is an adaptation of the one used by Lack and Eastwood (1962) and Eastwood *et al.* (1962) for studying bird migration and movements by radar films.

The principle involved is that the echo-signals displayed on a PPI scope during one complete horizontal scan are photographed on a single frame of a cine film. The echo-signals of a moving target which is hit during subsequent scans will be recorded in somewhat different places on following frames in a

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pattern correlated with the actual movement of the target. Since the duration of one scan, for example, at a range of 800 ft, takes about 24 sec, time on the cine film will be compressed to $\frac{1}{576}$. Projected at the regular speed of 24 frames /sec such a film allows one to view in $2\frac{1}{2}$ min the movements of fish during a period of 24 hr.

TECHNIQUES

As a horizontal echo-ranger the Honeywell sea scanner Model IB was used. This unit ranges from 0 to 400, 800, and 1600 ft, with possibilities of manual scanning over 240° and automatic scanning over 180 or 90° sectors. The operating frequency is 132 kc with the major lobe of the transducer radiating a conical pattern of 8° ($\pm 1°$) beam width. The visual presentation of the echo signals is displayed on two cathode ray tubes of which one is a 7-inch PPI scope with a grid for reading off relative bearing and range of the target (Fig. 1).

For time-lapse photography of the PPI scope an Arriflex 16 cine-camera with a single frame gear and variable speed motor was employed (Fig. 2). The frame transporting mechanism of the camera was connected with the transducer drive assembly in such a way that the film would be transported one frame at the end of each 180° scan. This was accomplished by installing two pairs of microswitches in the scan head, one pair at each extreme of the scan (Fig. 2). The microswitches were triggered by the scan alignment clamp (Fig. 2, No. 11), first the switch (Fig. 2, No. 12) starting the motor, followed by the switch (Fig. 2, No. 13) triggering the shutter. The stimulus duration of the shutter switch could be adjusted; this is necessary since the scan speed is not the same for the different scan ranges.

Since one frame is to be exposed during one complete scan of 180°, the movie camera requires a mechanism in which the shutter closes when the film is transported, but stays open in the rest position. The Arriflex 16 can be adjusted easily for such an operation by setting the shutter in the open position before connecting the single frame mechanism. Due to the construction of the camera, viewing through the lens is blocked with the single frame mechanism connected as described. Focusing on the PPI scope, therefore, has to be done before inserting the gear.

A watch with a black dial-plate and luminous numbers was mounted below the grid of the PPI scope so that the proper time would be recorded on every frame of the film (Fig. 1). This watch was dimly lit by a microscope light (Fig. 2, No. 8). The light intensity could be adjusted by a rheostat to the different time exposures for scanning at different ranges.

To avoid unwanted light, the space between the camera lens and the PPI scope was enclosed by a light-proof cover. This was accomplished by a combination of the Arriflex matte box and neoprene rubber sheeting as used for diving suits (Fig. 2, No. 5 and 6). The matte box allowed easy adjustment of the distance between camera and scope (which was about 18 inches using a 25-mm lens), while the neoprene cover simplified setting up and dismantling.

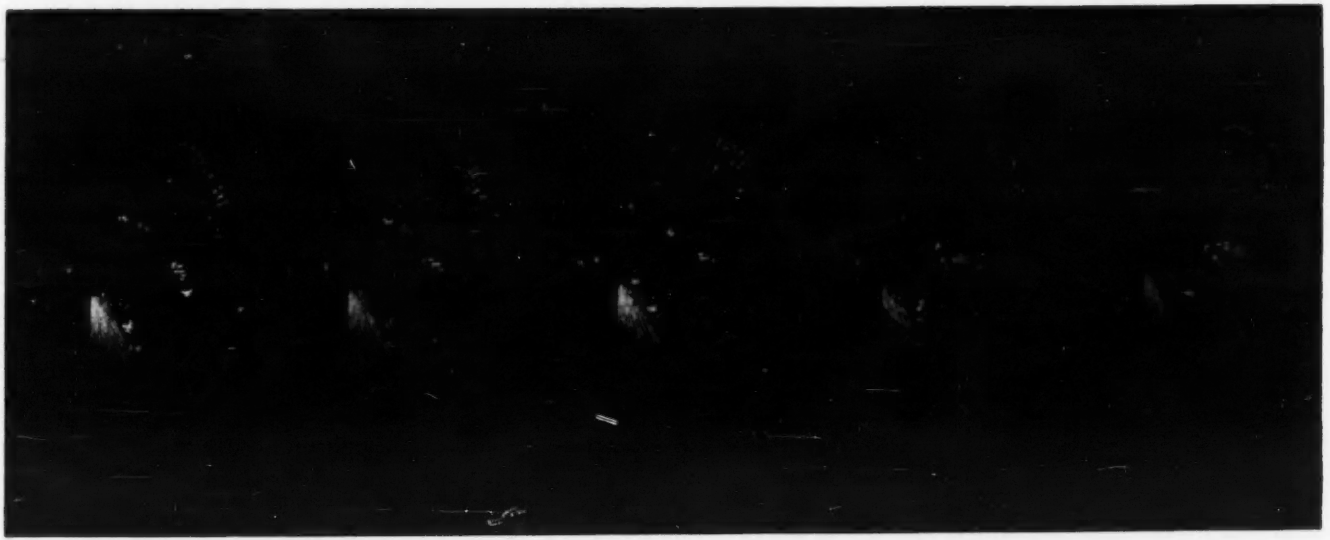

FIG. 1. Prints of every fourth frame of a strip of sonar film showing five successive stages of the movement of an apparent sockeye smolt school target (white arrow), Wolverine Point, May 30, 1963, 0726 hr, 400-ft range.

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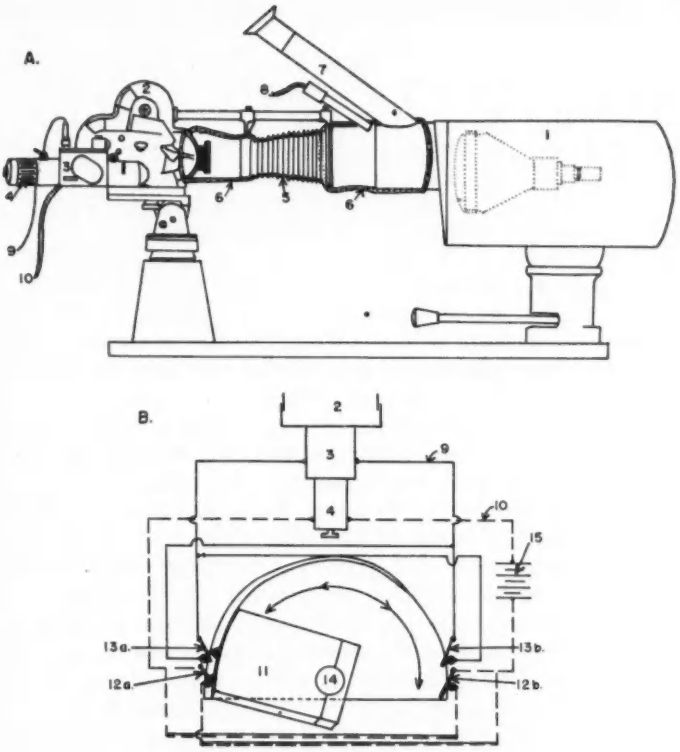

FIG. 2. A. Setup of time-lapse photography of PPI scope: (1) sea-scanner indicator, (2) Arriflex 16 cine-camera, (3) single frame gear, (4) variable-speed motor, (5) mattebox, (6) neoprene rubber covers, (7) viewing tube, (8) microscope light, (9) shutter release, (10) motor cable. B. Single frame circuit: (11) scan alignment clamp, (12 a, b) microswitches for motor, (13, a b) microswitches for shutter, (14) transducer drive tube, (15) battery for motor.

An observation tube (Fig. 2, No. 7) was mounted at an angle on top of the cover for watching the PPI scope while the camera was in operation. As mentioned before, once the single frame gear was connected to the camera, the PPI display could not be observed through the camera viewer.

Two types of film have been used so far, Tri X negative and Background X, both giving good results.

Operations were performed from a flatdeck self-propelled barge 24 × 10 ft. A tent was mounted on the barge housing all the equipment except the hull unit. The latter was installed in front of the barge on a swivel-type metal bracket so that it could be moved in a vertical plane from straight down to horizontally flat on the deck when not in use.

Power for the sea scanner was supplied by a portable light plant (1500 w). To get away from the vibrations and noise, this plant was mounted in a 10-ft

"pram" floating beside the barge. The camera motor and the microscope light were run from 6-v car batteries.

During scanning sessions the barge was tied to the shore in sufficiently deep water, or anchored down. It is essential that the gear be in a fixed position so that the same area is scanned each time. In general, scanning sessions were planned for 24 hr to obtain information on the diel pattern of migration. Once started the operation was completely automatic and, except for periodic checks of the power plant and changing of film, proceeded continuously throughout the time period of observation.

Analysis of the Sonar Films

To indicate the potentials of this technique, a few examples are presented, from the sockeye smolt migration in Babine Lake in north central British Columbia, Canada (Johnson and Groot, 1963).

For detailed analysis of the films a Bell and Howell time-motion projector Model IB was used. The echo-signals of fish targets on films taken during the first 15 min of every hour of operation were transferred to a sheet of paper with a grid similar to that of the PPI scope. Figure 3 represents such a diagram for the dusk period of intense sockeye smolt migration in Morrison Arm; arrows show the progressive change in position of targets, indicating movement during the 15-min period. Some of the smaller scale movements indicated by arrows may be open to question, but in many cases the progressive change in position is continuous over a rather great distance and appears without doubt to indicate definite migration.

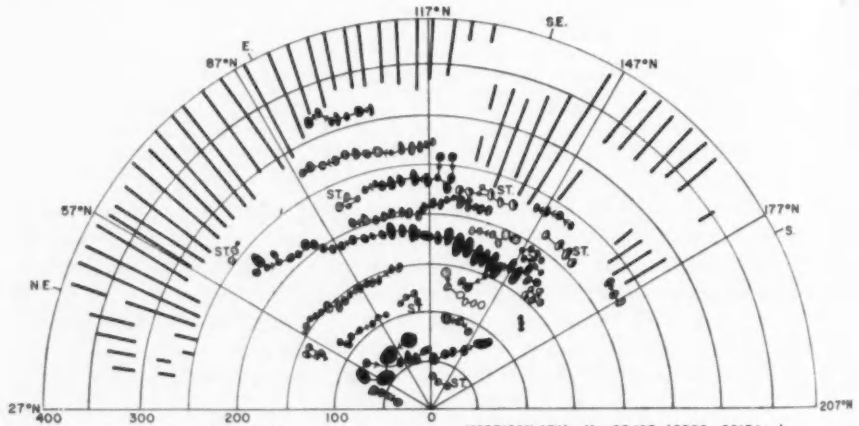

FIG. 3. Diagram showing moving and stationary targets taken off sonar film from 2200 to 2215 hr, Morrison Arm, May 23, 1963. Most targets, especially the moving ones, are considered to be sockeye smolt schools: ○ ⟶ ○ moving school, ● —— ● ST, stationary school, ////// bottom echoes.

Interpretation of Echo-Signals

Before the display on the PPI scope can be interpreted, a proper knowledge of the meaning of the different echo-signals must be acquired. Strongest arguments for considering certain echo-signals as ones indicating fish targets are obtained by direct identification. Due to the fact that sockeye smolt migration in fresh water occurs close to the surface during the dusk and dawn periods (Johnson and Groot, 1963), direct visual observations of surface activity could be made simultaneously with echo-signal display. This was done by two observers, one standing on the bow of the barge, calling off range, bearing, and direction of movement of sockeye smolt schools, and one watching the PPI scope display. In most cases the schools observed breaking the surface could be accounted for in terms of echo-signals. It is quite striking to see how, as soon as the first schools appear at the surface after sunset, the first moving echo-signals also appear on the scope.

An example of a target considered to be a school of sockeye smolts is presented in Fig. 1. The speed of movement of this target is about 160 ft in 144 sec or about 1.1 ft/sec. This brings us to another argument for identifying certain echo-signals as sockeye smolt schools, namely the similarity in average velocity between moving echo-signals and schools migrating near the surface (see section below on speed of migration). Of course, predators are often observed moving along with schools, and we have no means of distinguishing these on the sonar records.

Further arguments confirming target identification are the correlation existing between direction of movement at the surface and echoes from moving targets (compare Fig. 3 and 4), and the fact that when few moving sockeye smolt schools were showing at the surface during the dusk periods, few moving targets were displayed on the PPI scope.

Information on timing, intensity, speed, and direction of migration over 24-hr periods can be extracted from hourly series of such diagrams as presented in Fig. 3. When operations are extended through the whole migration period, seasonal variations of these parameters can further be obtained. Theoretically, it should also be possible, by employing suitable methods of calibration, to determine roughly the relative or approximate size of the sockeye smolt schools from the characteristics of the echo-signals.

Timing of Migration During a 24-hr Period

Projection of a 400-ft range sonar film at a speed of 24 frames/sec, speeds up the movements 288 times, and of an 800-ft range film 576 times. Viewing of the movies in this way revealed that the greatest concentration of moving targets occurred between 2130 and 2330, and between 0300 and 0500 hr PST during the last week of May. For the dates and latitudes (Babine Lake $\pm$ 55°N) at which these observations were made, sunset was around 2020 hr and sunrise around 0335 hr. Thus, most active migration of sockeye smolts in Babine Lake seems to commence about 70 min after sunset and 35 min before sunrise, each

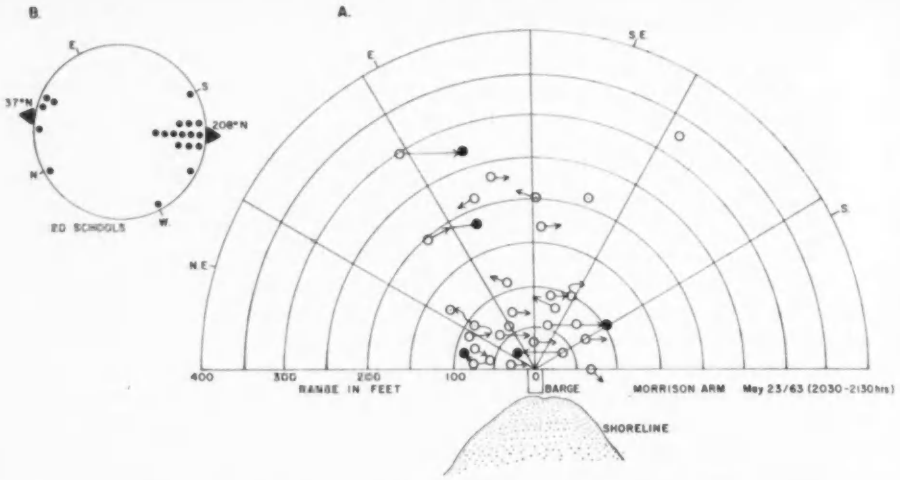

FIG. 4. A. Diagram showing near surface movement of sockeye smolt schools during the dusk period as recorded by direct visual observation, Morrison Arm, May 23, 1963, 2030–2130 hr, cloud-cover 50%. ○ ⟶ moving school, ● sounding school, ⊙ stationary school. B. Scatter diagram of the movements of the same sockeye smolt schools. The mean directional tendencies of the two modes are determined independently. (All ▶, $\bar{a}$ = $p < 0.05$.)

period lasting for about 2 hr. This estimate of timing of migration of sockeye smolts in the lake correlates closely with estimates based on catches at the outlet and with diurnal variations in two activities indicative of migration as observed in aquaria-held smolts (Johnson and Groot, 1963, fig. 5).

SPEED OF MIGRATION

The movements of sockeye smolt schools were transferred from the sonar film on paper on a grid similar to that of the PPI scope with a time-motion projector (Fig. 3). The sonar range was 400 ft (distance between center and circumference) and the time lapse between frames 12 sec, for this example from Morrison Arm, May 23, 1963. From the distance between first and last echo-signal of each tract and the time elapsed (computed from the total number of frames the target could be followed minus one) the speed of movement was calculated.

The average speed of movement of 18 schools migrating between 2200 and 2215 hr (early evening) was from 0.53 to 2.44 ft/sec with an average of 1.05 ft/sec. Between 0100 and 0115 hr velocity of swimming was from 0.23 to 1.59 ft/sec with an average of 0.81 ft/sec. During the late-dawn early-morning period from 0600 to 0615 hr, the speed of movement of nine schools varied between 0.30 to 1.43 ft/sec, with an average of 0.82 ft/sec.

Direct measurements of speed of near-surface migrating schools revealed velocities between 0.65 and 1.0 ft/sec with a mean of 0.8 ft/sec during the

dusk period (Johnson and Groot, 1963). The sonar film measurements for about the same period give a mean speed of 1.05 ft/sec.

Brett *et al.* (1958) have shown that, under experimental conditions, sockeye juveniles of this size range are capable of maximum sustained swimming speeds of 0.8–1.0 ft/sec in the temperature prevailing in Morrison Arm during migration time. This suggests that sockeye smolts swim at their maximum sustained level during migration when compared with the experimental results.

Direction of Migration

From diagrams as shown in Fig. 3 for the early-evening migration of sockeye smolts in Morrison Arm, directional tendencies can be determined. In cases where the path of swimming was not on a straight line, the direction of the first few echo-signals of a tract were taken. For further analysis the directions of swimming were plotted in circular scatter diagrams. Figure 5 presents directions of movements of sockeye smolts for the early evening, night, and early morning periods in Morrison Arm.

The 2200–2215-hr period (Fig. 5A) shows concentrations of swimming directions between W and SW (mean 237°N) and between NNW and NE (mean 9°N). The means for these two modes of directional tendencies are determined separately by vector addition, and the departure from uniformity calculated as described by Schmidt-Koenig (1961). A comparison of these preferred swimming directions with the compass direction of Morrison Arm is presented in Fig. 6. The SW to W tendency is appropriate as far as reaching the outlet of Babine Lake is concerned, and correlated with directional preferences as found under experimental conditions for the same time of the season (Johnson and Groot, 1963).

Two possible interpretations can be given for the northerly migrating schools: Firstly, they can be considered as "reversed migration," a phenomenon common in migrations of many animals. Direct observations of near-surface migration during the dusk period of May 23, 1963, in Morrison Arm, also indicated some movement in the opposite direction to the main portion of schools (Fig. 4). Secondly, the NNW to NE movements can be attributed

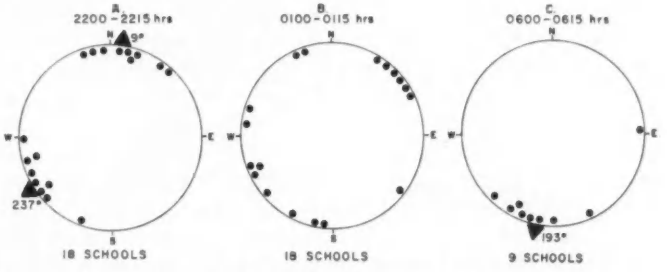

FIG. 5. Scatter diagrams of direction of movement of targets during A. early evening (2200–2215 hr) (same data as shown in Fig. 3), B. night (0100–0115 hr), and C. early morning (0600–0615 hr). Morrison Arm, May 23–24, 1963. (All ▶, $\bar{a}$ = $p < 0.05$). All targets are considered to be sockeye smolt schools.

to sockeye smolt schools from the main lake population which, during their migration to the outlet, ended up in the wrong arm — Morrison Arm instead of the North Arm (Fig. 6). Indeed, some sockeye smolts captured, tagged, and released up-lake at Sandspit (Fig. 6) have been recovered at a trap at the head of Morrison Arm during mark recovery operations in 1962 (W. E. Johnson, personal communication).

No obvious directional tendencies are evident for the 0100–0115 period (Fig. 5B). The early morning swimming directions of sockeye smolts between 0600 and 0615 hr show a mean for a SSW direction (Fig. 5C) which, in view of the migration along the shortest route to the outlet, is the expected one.

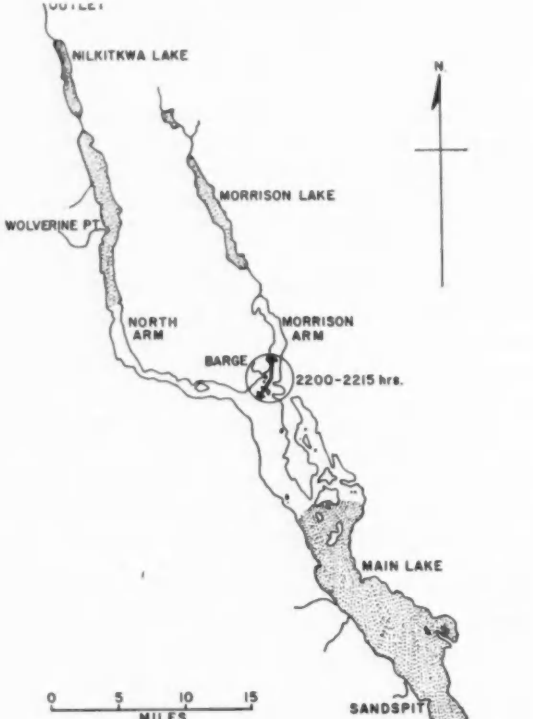

FIG. 6. Map of Babine Lake and adjacent waters. Arrows indicate mean directional tendencies during early evening (2200–2215 hr) on May 23, 1963, in Morrison Arm. Dotted areas indicate distribution of sockeye smolts prior to migration to outlet.

The correct interpretation of the significance of the different directional tendencies, however, does not concern us here; what should be stressed is that the sonar observations reveal information on migration patterns below the surface and during times when direct observation would not be possible due to low light intensities, or migration of smolts at depth.

CONCLUSION

One of the main reasons for the progress in science during the last century has been the ability of man to extend observations beyond his own rather limited sensory capacities. Echo-sounding and echo-ranging are an outstanding development of new tools for long-range observations on distribution and movements of fishes. The technique described in this paper, in which sonar is combined with time-lapse photography, shows an effective way of obtaining information on movements of fishes, as indicated by the few examples given of analysis of movies taken of sockeye smolt migration.

To date the analysis of the sonar films of sockeye smolt migration has not revealed anything which was not already known by using other techniques (Johnson and Groot, 1963). This is mainly because this migration can be observed so readily near the surface during the dusk period, and that information on seasonal and diurnal migration patterns can be obtained by trapping operations at the lake outlet. This technique will be even more useful when the migration or movements under study are not as readily observable as those of sockeye smolts.

With experience, a high degree of accuracy should be possible in interpreting sonar PPI scope displays (see Sec. 11, pp. 474–527, in Modern Fishing Gear of the World, 1959) in studies of fish migrations. Workers studying migration by radar have already shown this for similar types of displays (Sutter, 1957; Tedd and Lack, 1958; Lack and Eastwood, 1962; Eastwood *et al.*, 1962).

Of course there are a number of greater inherent difficulties when working on fish migrations with sonar than with studies of bird migrations using radar. Firstly, the speed of sound in water is only about 4900 ft/sec, while the speed of radio waves in air is 186,000 miles/sec. This makes the range and rate of scanning much more restricted in water. Secondly, water masses contain resident populations of fishes and other organisms, which are always potential targets and may greatly outnumber the mass of migrating fish targets, whereas air does not contain comparable permanent communities of living organisms at relatively high altitudes. Thirdly, except over water masses remote from shore, there is no problem of locating a stable platform for radar observation installation. In contrast, the short range of sonar gear and the difficulty of establishing a stable platform offshore are objects of major limitation. Nevertheless, future potential use of sonar in the study of fish migrations can be viewed with some optimism.

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Our thanks are also due to Dr D. Lack for the information given on the technique of time-lapse photography of radar PPI displays.

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The Role of Behavior in the Ecology and Interaction of Underyearling Coho Salmon (*Oncorhynchus kisutch*) and Steelhead Trout (*Salmo gairdneri*)[1,2]

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ABSTRACT

Two similar salmonids, coho and steelhead, cohabit many coastal rivers of British Columbia. Field collections reveal that the distributions of underyearling coho and steelhead are similar along the length of these streams. However, the micro-distribution of the two species is different. In spring and summer, when population densities are high, coho occupy pools, trout occupy riffles. In autumn and winter, when numbers are lower, both species inhabit the pools. Nilsson (1956) stated that segregation (such as that shown by coho and trout in spring and summer) may be indicative of competition resulting from similar ecological demands. To test this hypothesis the distribution and behavior of coho and steelhead were compared in a stream aquarium at different seasons with gradients of light, cover, depth or depth/velocity, and in experimental riffles and pools. Distributions and preferences of the two species in the experimental environments were most similar in spring and summer, the seasons when segregation occurred in nature, and least similar in autumn and winter, the seasons when the two species occurred together in nature. Spring and summer segregation in the streams is probably the result of interaction which occurs because of similarities in the environmental demands of the species and which is accentuated by dense populations and high levels of aggressiveness. The species do not segregate in streams in winter because certain ecological demands are different, numbers are lower, and levels of aggressiveness are low. When the two species were together in the experimental riffle and pool environment, trout were aggressive and defended areas in riffles but not in pools; coho were aggressive in pools but less inclined to defend space in the riffles. These differences in behavior probably account for the distribution of trout and coho in natural riffles and pools.

The data support the basic contention of Nilsson (1956) and illustrate the role of behavior in segregation produced by competition for space.

INTRODUCTION

Two similar species of salmonids occur together in many of the coastal streams of British Columbia. These fish, coho salmon (*Oncorhynchus kisutch*) and steelhead trout (*Salmo gairdneri*), resemble each other in several respects. Both coho and steelhead are anadromous. Young coho remain in the streams where they hatch for 1 or 2 years, steelhead may remain in the stream up to 3 years. In addition, they are similar in size and morphology. On the basis of present concepts, they are potential competitors.[3]

[1]Received for publication December 28, 1964.

[2]Based on a thesis submitted in conformity with the requirements for the degree of Doctor of Philosophy at the University of British Columbia.

[3]The meaning of competition, when used in this paper is, "The demand, at the same time, of more than one organism for the same resources of the environment in excess of immediate supply" (Milne 1961). The meaning of niche is as given in DeBach and Sundby (1963).

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Young coho and steelhead coexist along the lengths of streams, but within each stream they occur in different microhabitats. Their ecology is given more fully in the text. To introduce the problem, it is sufficient to note that microhabitat segregation is pronounced in the spring when population densities are high and breaks down during fall and winter when population levels are low.

Nilsson (1956) developed valuable concepts which may provide an explanation for the separation of coho and trout during spring and early summer. He postulates that allopatric populations of closely allied species, or species having similar ecological demands, utilize the full range of their ecological potentials under conditions of intense intraspecific competition. Intense interspecific competition in sympatric populations of similar or closely related species forces each species to compete only at its "ecological optimum," i.e. under those conditions to which it is best adapted or where it has some competitive advantage. It is this tendency of species to utilize only their ecological optima that results in segregation during rigorous interspecific interaction.

On the basis of Nilsson's ideas it seems likely that certain environmental requirements and aspects of behavior of young trout and coho may be more similar in spring and early summer than during fall and winter. Accordingly there are two objectives to this study. The first is to obtain and present data from the field study outlining in some detail the period and nature of interspecific segregation. The second objective is to compare, under partially controlled conditions, the environmental responses, preferences, and behavior of young coho and trout, and to determine if segregation occurs when these are most similar. Essentially this involves testing Nilsson's ideas (Nilsson, 1956, 1963) under controlled conditions. If the species are segregated at that period when requirements are similar, attempts will be made to ascertain the role of behavior in this interaction. Newman (1956), Lindroth (1955a), Kalleberg (1958), and Nilsson (1963) have shown how behavior enters into interspecific competition. It is not clear, however, what type of behavioral mechanism functions to give one species an advantage over the second species in one situation and for this advantage to be reversed in another situation.

The research is described in two sections; the first deals with studies under field conditions, the second deals with studies in a partially controlled environment. Methods and Results are within each section.

FIELD STUDY

Description of Study Area

Three rivers in the lower Fraser valley of southwestern British Columbia were studied (see insets of the Chilliwack, Alouette, and Salmon Rivers in Fig. 1).

CHILLIWACK RIVER

The Chilliwack River rises in the Cascade Range in Washington and drains north into Chilliwack Lake (elevation 620 m), thence it flows west

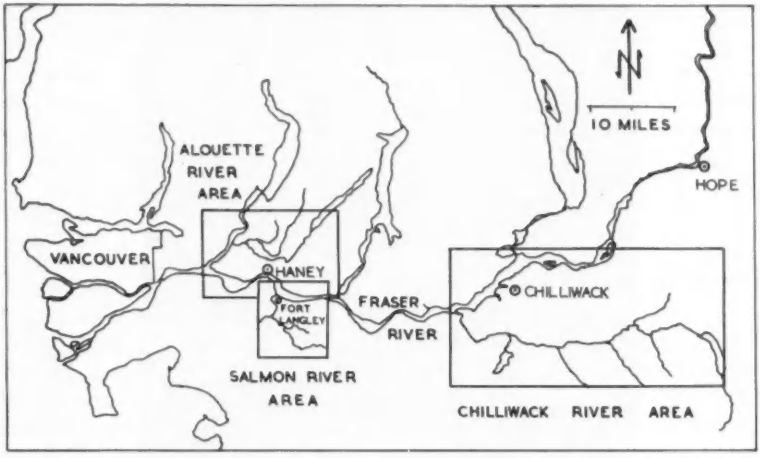


FIG. 1. Lower Fraser valley area in southwestern British Columbia showing Alouette, Chilliwack, and Salmon River systems.

into the Fraser River. Figure 2 shows the portion of the river studied and station locations.

The river runs through a deep valley in a stable rock channel from Chilliwack Lake to the region at V-28 (Fig. 2). Large areas of the upper river are covered with extensive log jams (Fig. 3,A). In the middle stretches of the river (V-28 to V-13), the channel bottom is less stable and large log jams are absent (Fig. 3,B). Several large tributaries (Slesse, Foley, Chipmunk, and Tamihi Creeks) enter this stretch of the river. The discharge of these tributaries fluctuates considerably, hence, below V-13 the channel is braided and much

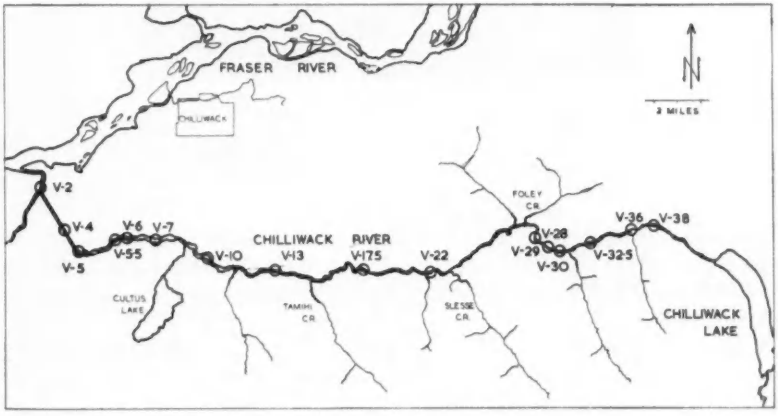


FIG. 2. Chilliwack River and location of stations.

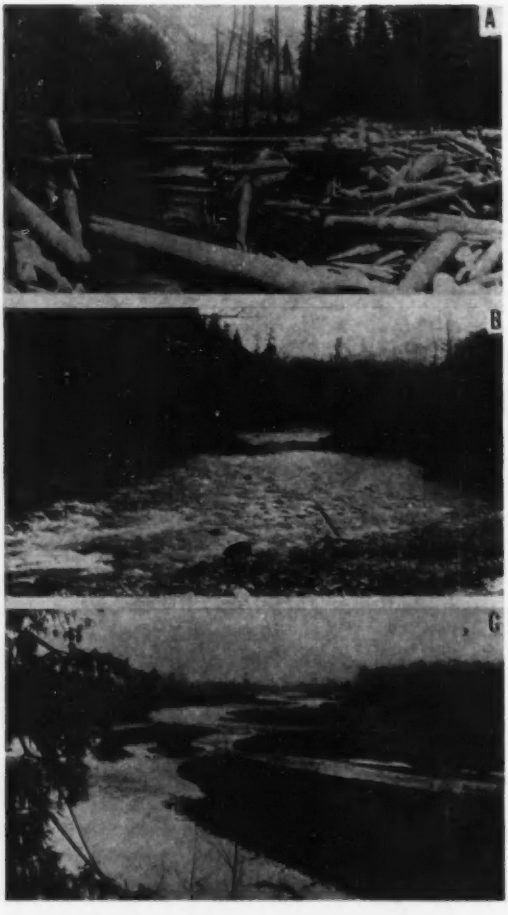


FIG. 3. A. Upper Chilliwack River in area of large log jams, V-36 to V-38. B. Chilliwack River in the region of V-17.5. C. Chilliwack River at V-5.5 and V-6. Note braided channel and unstable gravel bars.

of the bottom is unstable (Fig. 3,C). There is one log jam near V-5. The lowermost region of the river travels across flat terrain and the bottom is composed of unstable sand and gravel. Much of the channel is modified and dyked (see V-5 to V-2, Fig. 2).

The Chilliwack River drains an area of 1250 km^2. Between 1958 and 1962, highest flows occurred during two periods each year. In the first peak in May or June mean monthly flows ranged from 105 to 184 m^3/sec. In the second peak, October to January, mean monthly flows ranged from 62 to 96

m^3/sec (data from the Water Resources Division of the Department of Northern Affairs and National Resources).

During 1960, 1961, and 1962, mean monthly water temperatures ranged from a low of 2 C in January to a high of 13 C in August. (Details of temperature and discharge in the Chilliwack, Alouette, and Salmon Rivers are recorded in the thesis upon which this publication is based.)

ALOUETTE RIVER

The South Alouette River originates at the west end of Alouette Lake. It drains west into the Pitt River, a tributary of the Fraser. Figure 4 shows stations along the portion of the river which was studied.

The upper river (A-16 to A-9) runs down a shallow valley through big pools and stretches strewn with large boulders (Fig. 5,A). The stream bottom is relatively stable in most areas above A-9. From A-9 to below A-6 the river passes through flat terrain in a channel with an unstable rock and gravel bottom. In this region the river bed has been modified considerably to prevent flooding (Fig. 5,B). Lower sections of the Alouette (A-3 to A-0) lie in meadowland (Fig. 5,C). The stream bottom is composed of fine gravel, sand, and mud. Log jams are absent along the full length of the river.

The Alouette River drains an area of 205 km^2. During 1960, 1961, and 1962, highest mean monthly flows, 5.2–9.8 m^3/sec, occurred in January. Lowest discharges occurred in July and August and ranged from 0.2 to 0.4 m^3/sec. Although mean monthly discharges in winter are quite low, the Alouette River occasionally freshets violently, changing from flows of 2–3 to 112 m^3/sec over a period of 5 or 6 days (data from Water Resources Division of Department of Northern Affairs and National Resources).

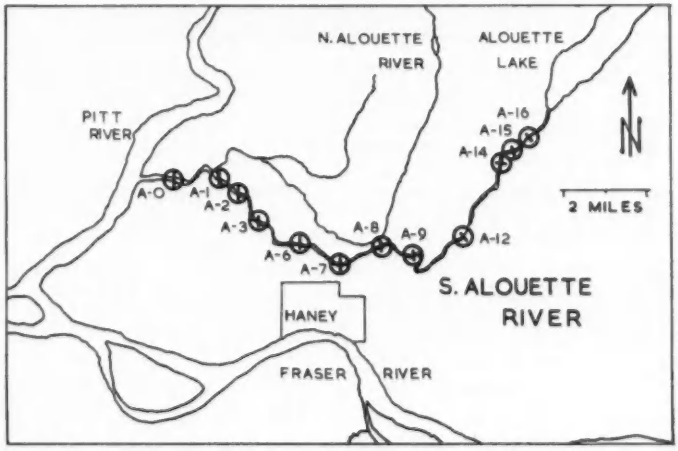


FIG. 4. Alouette River and location of stations.

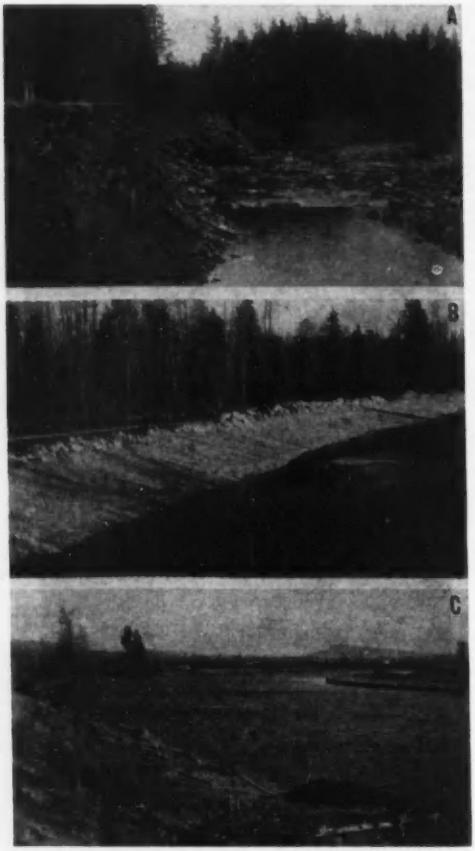


FIG. 5. A. Alouette River at A-12, channel with large boulders on bottom and with stretches containing large pools. B. Alouette River at A-7. Note gravel bottom and modified channel. C. Alouette River at A-2 in meadow and farm land.

Mean monthly temperatures, during 1960, 1961, and 1962, ranged from 2.8 C in January to 20 C in July.

SALMON RIVER

The Salmon River rises in low wooded farmland, northeast of Langley, British Columbia, at an elevation of about 100 m. Figure 6 shows the location of stations along the Salmon River.

The upper tributaries of the river lie in small valleys and have stable channels (see S-12 to S-19, and S-10 to S-18, Fig. 6). The middle section of the river lies in almost flat surroundings in a sand and gravel bed (Fig. 7,A). Below S-6 the river meanders through meadows in a mud and sand channel.

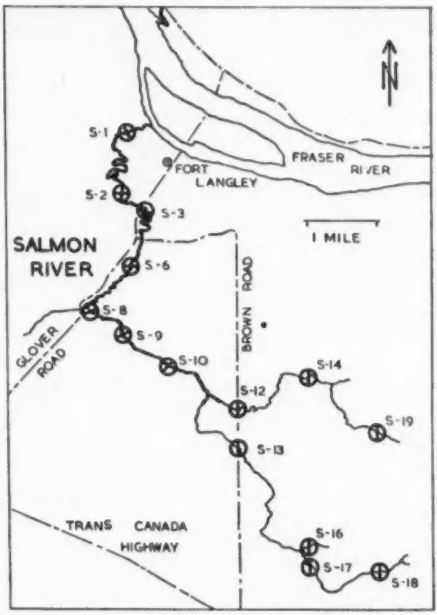


FIG. 6. Salmon River showing location of stations.

The overall character of the flow is gentle, with much of the river consisting of ripples and pools lying in well-wooded areas (Fig. 7,B).

The Salmon River drains an area of 83 km^2. Mean monthly flows (based on Water Resources Division data) reach a peak between November and February. In 1960, 1961, and 1962, mean monthly flows ranged from 0.23 m^3/sec in July and August to 5.9 m^3/sec in January and February. During winter, large short-term fluctuations in discharge occur, e.g. from 0.85 m^3/sec on January 23 to 8.32 m^3/sec on January 25, 1960.

In the Salmon River, during 1960, 1961, and 1962, mean monthly temperatures ranged from 3.2 to 3.8 C in December and January, and from 12.9 to 15.5 C in June, July, and August.

The three rivers studied contain a variety of types of habitat. These habitats ranged from small, low-elevation tributaries with gentle flows, to large, rapid, and turbulent rivers. Bottom conditions in each stream vary from unstable sand and gravel to stable gravel or boulders. In the field work dealt with in the next section, fish collections were made over the full range of conditions described for the three streams.

MATERIALS AND METHODS

Young coho salmon and steelhead trout were studied in three lower mainland rivers of British Columbia, the Chilliwack River (Fig. 2), the Alouette

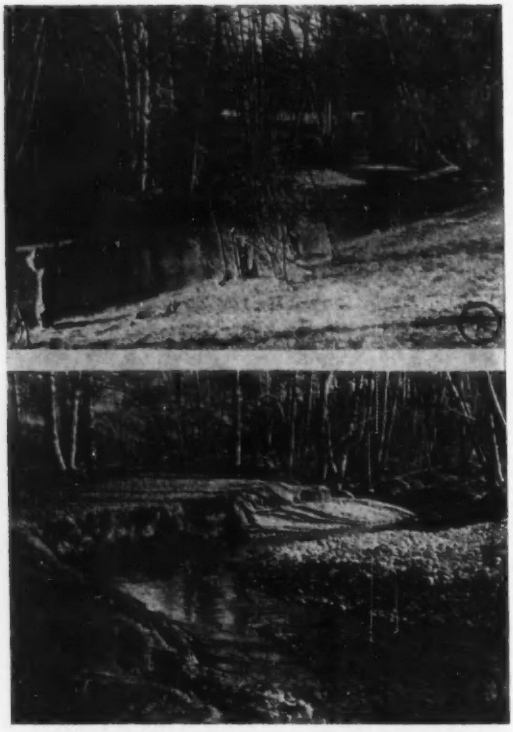


FIG. 7. A. Salmon River at S-9. B. Riffle and pool areas at S-14.

River (Fig. 4), and the Salmon River (Fig. 6). Twelve to 16 stations per river were visited about once a month from November 1959 to March 1962.

A routine collection procedure was followed if conditions permitted. Fish were always collected by seining in the Salmon River and wherever possible in the larger rivers. In addition C.I.L. "Prima Cord," a detonating fuse, and electrical blasting caps were used to collect fish among the large boulders and under log jams. The explosive was detonated in the stream above a set seine net and the fish drifted into the seine; the blast area (usually small) was searched.

Records, kept on a standard data sheet and a sketch map for each station, included number of fish collected and approximate area of stream bottom sampled. Temperatures were taken by Weksler temperature recorders. Stream velocities were calculated from the rate of movement of floating objects. Turbidity and bottom composition were recorded on a rough quantitative basis. In addition, distribution data based on collections were supplemented with a series of diving observations in the Chilliwack River. In each diving census the number, behavior, and distribution of fish were recorded in three

standard census strips on the stream margin at V-28 and V-30. Each strip was 67 m (200 ft) long and about 1 m wide.

Results

Longitudinal distribution in streams

Highest densities of young steelhead trout and coho in the Chilliwack occurred in the upper reaches of the river (Fig. 8). High densities recorded in Fig. 8 (V-29 to V-38) were not necessarily representative of the entire upper river. However the type of habitat where highest numbers were recorded (large log jams) was characteristic of the upper part of the Chilliwack. In this region, the river bed was more stable and offered better shelter to fish. For this reason numbers of fish at stations V-22, V-28, and V-30 (Fig. 8), where log jams were absent, were higher than those at comparable locations (V-17.5, V-13, and V-10) in the lower half of the river (Fig. 8). In the downstream portions of the Chilliwack (below V-10) where the bottom was unstable and the channel was braided, numbers of both species were lowest. The relative numbers of trout and coho and the general distribution pattern were the same in winter as in the period from March to September (Fig. 8). At most stations, coho were more abundant than steelhead. During the early summer young coho were captured further downstream than steelhead; but aside from this the two species were distributed in a similar fashion along the length of the river.

In the Alouette River, greatest concentrations of coho and steelhead occurred at stations A-9, A-12, A-14, and A-15 (Fig. 9), all of which are characterized by a cover of heavy boulders (Fig. 5,A). Below A-9 in areas with mud, sand, or unstable gravel bottom (Fig. 5,B and C), densities were low

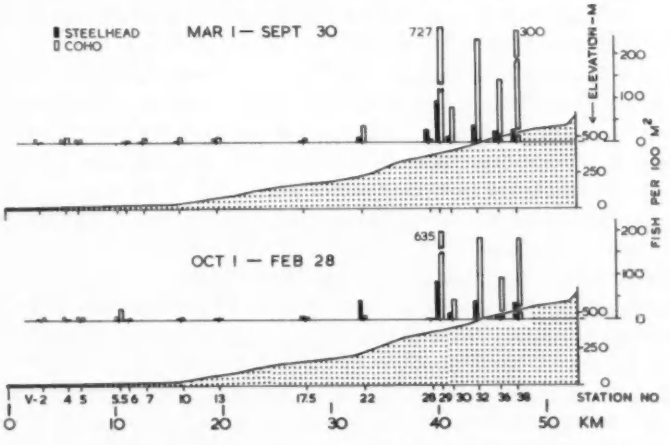


FIG. 8. Density and distribution of young coho and steelhead in the Chilliwack River (data combined for period from November 1959 to March 1962).

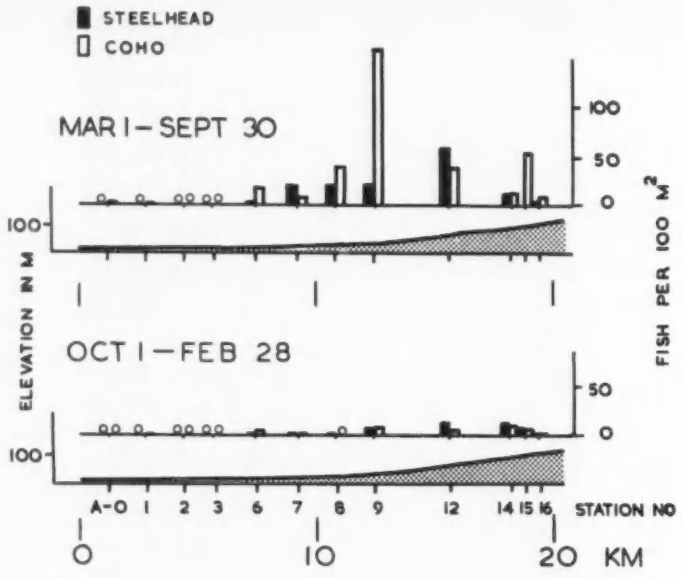


FIG. 9. Density and distribution of young coho and steelhead in the South Alouette River (data combined November 1959 to March 1962).

(Fig. 9). During the winter, density of both species was reduced to a low level, probably due to violent winter freshets which scoured the river periodically. In the period March 1 to September 30, coho fry were distributed further downstream than steelhead. Figure 9 shows that, although relative numbers of trout and coho varied at different stations, both species were distributed together along much of the river.

In the Salmon River, unlike the Chilliwack and Alouette Rivers, young coho occurred with young steelhead trout and cutthroat trout (*Salmo clarki*). It was not possible to identify and separate the two trout species during their first few months of life. Reference to trout in the Salmon River therefore includes some cutthroat as well as steelhead.

Highest densities of young trout and coho were recorded in the upper part of the Salmon River (S-9 to S-18, Fig. 10) and in its upstream tributary (S-12 to S-19, Fig. 10). This area of the river was characterized by small pools and gentle riffles (Fig. 7, A and B). Much of the shoreline was overgrown and covered with fallen trees. Below S-8 the bottom was composed of unstable gravel or sand and mud; numbers of coho and trout in this area were lower (Fig. 10). In early summer young coho were distributed down the Salmon River into the mud bottom portions of the stream at S-2 and S-3. Coho densities were higher than trout at all stations, but both species occurred together over most of the length of the stream (Fig. 10).

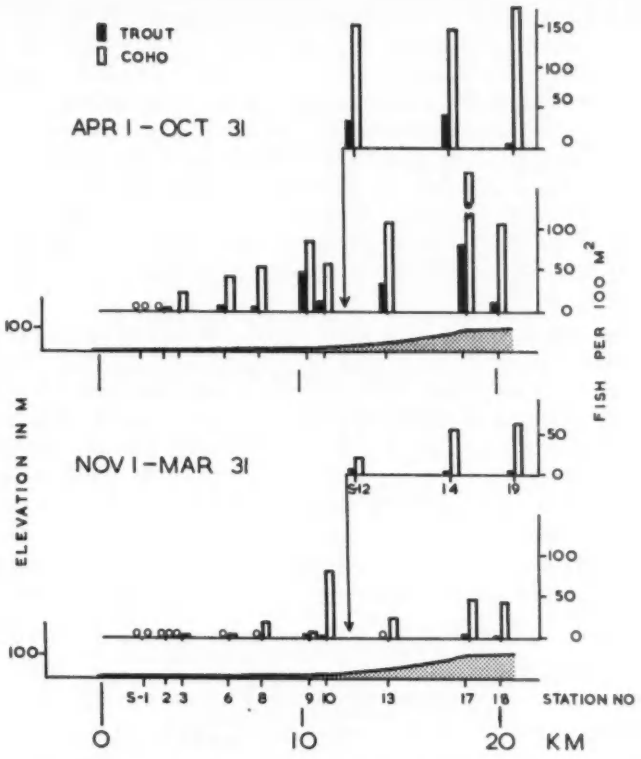


FIG. 10. Density and distribution of young trout and coho in the Salmon River (data combined November 1959 to March 1962). Broken bar in upper part of Figure represents 466 coho.

A variety of types of physical habitat was studied within each of the three rivers. Furthermore, size, bottom, and flow conditions differed considerably among the streams. Methods of sampling were not the same in all rivers. In spite of such differences in habitat and sampling the two species exhibited comparable distribution patterns in each of the three rivers (Fig. 8–10). Trout and coho cohabited the lower sections of the streams in low numbers and occurred together in highest numbers in the more stable environments near the headwaters or headwater lakes.

MICROHABITATS OF UNDERYEARLING COHO AND TROUT

In the Chilliwack and Salmon Rivers, young coho and trout exhibited seasonal changes in choice of microhabitat. In the Alouette River it was not clear whether or not changes in choice of microhabitat occurred at different seasons.

Recently-emerged trout and coho in the Chilliwack occupied three types of microhabitat: shallow water in small bays at the stream margin, small shallow riffles, and small crevices about the inshore portions of log jams and large boulders. The distribution changed during summer and early fall. By late fall most coho were located under log jams or under overhanging banks and boulders; steelhead occupied the rocky areas of the stream margin and the log jams. Figure 11 shows the density of steelhead and coho in relation to log jam cover during 3 seasons. A pronounced seasonal reduction in density occurred in areas where heavy log cover was absent. During winter those fish utilizing areas where log cover was absent were found only under or among the boulders.

In cases where young coho were found among the large stones at the stream margin, their distribution did not extend far from shore. Young trout on the other hand were seen and collected among the boulders as much as 8 m from shore. Steelhead were able to occupy a wider variety of microhabitats in the Chilliwack River. The species composition in each of the two microhabitats distinguished in Fig. 11 was approximately the same at all seasons but steelhead made up a larger fraction of the fish taken in the areas where log cover was absent than where it was present (Fig. 11).

In the Salmon River, recently-emerged coho and trout became segregated, with regard to microhabitat, during the first 2 months (Fig. 12). Trout density

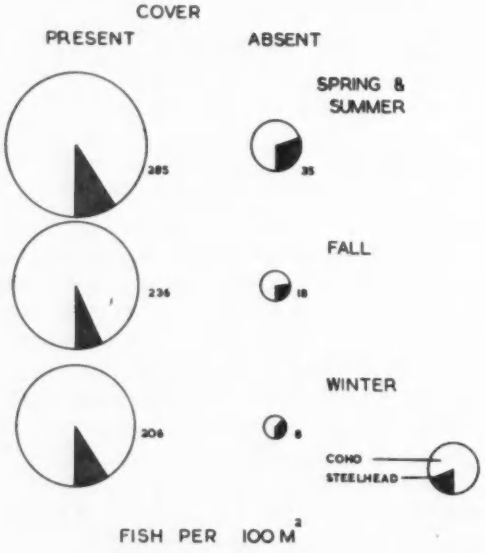


FIG. 11. Densities of young coho and steelhead in areas where cover (log jams) is present compared to areas where cover is absent. Data from the Chilliwack River, November 1959 to March 1962.

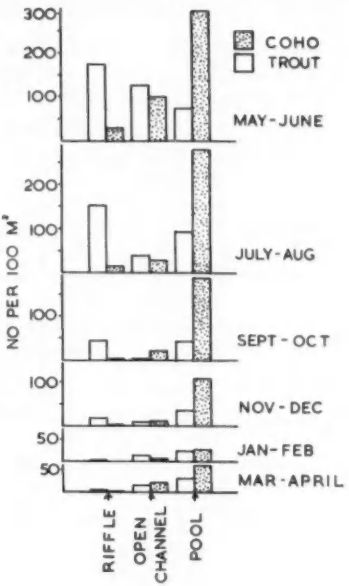


FIG. 12. Densities of young trout and coho in three types of stream habitat, riffle, open channel, and pool, during six periods of the year. Data from the Salmon River, November 1959 to March 1962.

was highest in the riffles and lower in the open channel habitats and pools throughout May–August. In this period coho densities were highest in the pools and lowest in the riffles. The density of fish decreased through the first 10 months (Fig. 12). In the fall and winter, when numbers of fish were lowest, the degree of habitat segregation was reduced. By January and February coho and trout exhibited the same pattern of microhabitat distribution (Fig. 12).

SIZE RELATIONSHIPS OF FISH IN THE SALMON RIVER

Coho began to emerge in late March, while the first trout emerged in early June. Because of this difference in hatching time, coho were larger than trout in June and July (Fig. 13). This size discrepancy decreased during late summer and autumn until, by winter, the size ranges were alike (Fig. 13). Virtually all coho migrated out of the Salmon River in May and June, at age of about 14 months. Trout remained in the river 2 years or more. Winter samples of trout could be separated into underyearling and "1 year plus" fish using length frequency plots of all trout (Fig. 14). Fish over 85 mm were designated as 1 year or more in age.

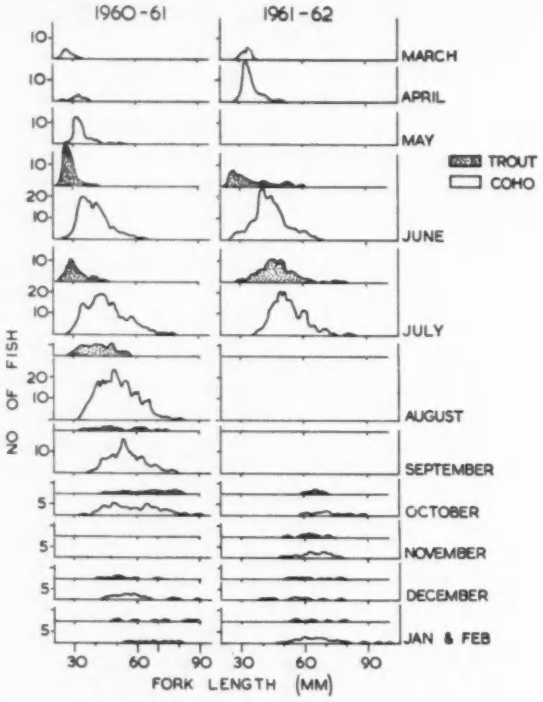


FIG. 13. Size relationships of underyearling trout and coho in the Salmon River. Smoothed curves are based on moving averages of three, data before smoothing was plotted in 1-mm length intervals.

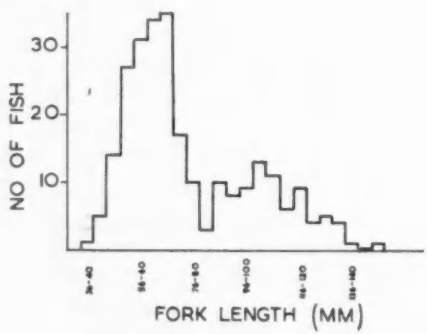


FIG. 14. Length frequencies of two or more year-classes of trout in the Salmon River. Data are lumped, October to February inclusive, for 3 winters.

SUMMARY AND COMMENTS

Field data show that trout and coho occur together along the lengths of the three streams. They are, however, found in different microhabitats within the streams. The differences in microhabitat distribution are most distinct in the small stream, the Salmon River, where trout and coho are segregated in riffles and pools in spring and summer, but to a large degree occur together in pools in winter.

This case, where segregation occurs at one season but not at another, provides a good situation where Nilsson's (1956) concepts may be tested. However, fish are difficult to observe and environmental conditions cannot be controlled in the natural stream habitat. For this reason the investigation was brought into the laboratory where fish could be studied in a stream aquarium; the second part of this paper describes the experimental facilities and the methods of comparing the distribution and behavior of the two species. Field results are discussed in the light of experimental data.

STUDY UNDER CONTROLLED CONDITIONS

MATERIALS AND METHODS

HOLDING CONDITIONS AND FISH

The experimental study was conducted between October 1962 and December 1963 in the Puntledge Park Hatchery at Courtenay, British Columbia.

The coho salmon were obtained from Little River, a small stream near Comox; the steelhead were from Big Qualicum River near Parksville. All fish were captured with seine nets. Fish used in the first series of observations (November 1, 1962, to February 20, 1963) were captured during October 15–22, 1962. Coho used in experiments between April 19 and October 9, 1963, were seined April 11–23, 1963. Trout used in work from June 9 to October 9, 1963, were obtained May 25, 1963. Size range and mean fork lengths of samples of fish, measured at several intervals during the work, are given in Appendix I.

All fish were held in running water in painted plywood troughs, 40 cm wide and 220 cm long. The troughs were housed in black plastic chambers and illuminated with fluorescent lights.

Fish used in spring and fall experiments were held at a 12-hr day length (see Appendices II and III), those used in winter experiments were held at a 12-hr day — subsequently reduced to 8 hr (see Appendix IV).

Water used in holding troughs and stream aquarium came from the City of Courtenay mains. Water temperature increased during spring and early summer, declined gradually during autumn and dropped to 0.5 C or less in winter (Fig. 15). Stream aquarium temperature in Fig. 15 will be referred to later in the text. The sharp rise and 3-day temperature peak, December 3–6 (Fig. 15), occurred when a break in the city water main forced the use of an alternate supply.

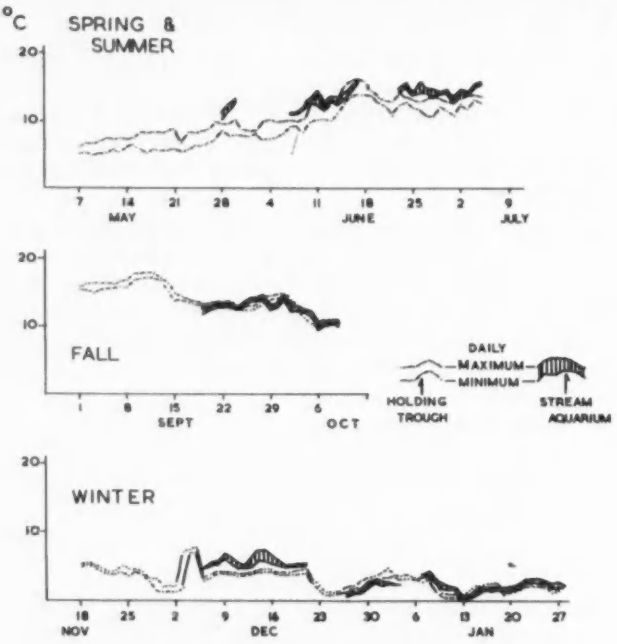


FIG. 15. Temperature maxima and minima (daily) in the stream aquarium during seasons in which the study was made (solid lines). Breaks in the line indicate that no experiments were in progress. Dotted lines represent temperature maxima and minima in holding troughs plotted for 2 weeks or more previous to experiments.

Fish in the troughs were fed a diet (by weight) 21% liver, 65% drained canned salmon, 8% brewer's yeast, 6% pablum, and salt (about 1 teaspoonful for 300 g of food). This food mixture was ground into a paste, frozen for storage, and fed in the form of frozen scrapings. Fish were fed once daily and remained healthy throughout the study.

DESCRIPTION OF STREAM AQUARIUM

The stream aquarium was designed to represent a short section of a small stream. Dimensions of the unit are 6.3 m long, 2 m high, and 1.2 m wide with an observation area 5 m long and 0.7 m deep (Fig. 16).

Most of the aquarium is made of 1-inch (2.5-cm) plywood supported in a framework of 2-inch × ¼-inch (5.1 × 0.6-cm) angle iron. The windows are ⅝-inch (1.6-cm) plate glass. Construction of the axial-flow pump required a strong, nontoxic, rust-resistant material. This portion of the aquarium was therefore made of ⅛-inch (0.3-cm) welded mild steel lined with ⅛-inch (0.3-cm) fiber-glass reinforced plastic.

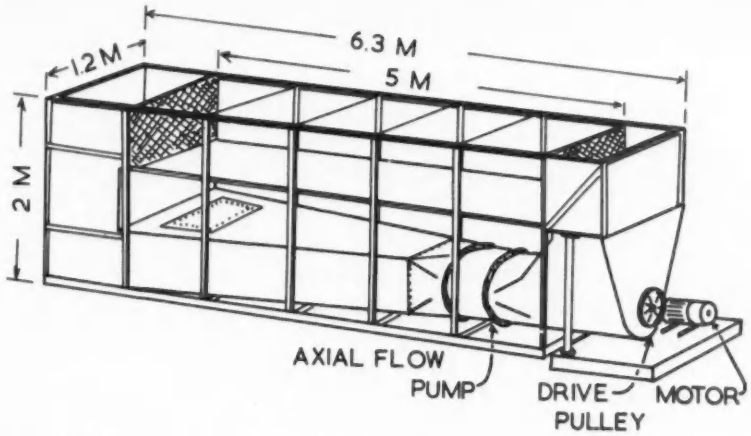


FIG. 16. Experimental stream aquarium. Details of the drive mechanism are not shown.

Current in the stream aquarium could be maintained at the desired velocity with a variable-speed-drive mechanism. Water level was adjusted with an inlet hose and a series of drain pipes. Water was circulated from the pumps along the tapered duct at the bottom of the unit, up at the end opposite the motor, and along the observation flume back to the pump.

The apparatus was lighted from overhead by parallel fluorescent lights running the full length of the observation flume.

An observation gallery of black polyethylene sheeting paralleled each side of the tank. Adjustable horizontal slits in the plastic facing the aquarium permitted observation from the darkened galleries without disturbing the fish.

DESCRIPTION OF EXPERIMENTAL ENVIRONMENTS

Behavior and distribution of fish were compared in a control environment, in four different environmental gradients, and in a riffle-pool environment. The following is a description of these arrangements and some of the conditions associated with them.

Figure 17 shows lateral aspects and plan views of control and four gradients. In the *control situation* (Fig. 17,a) the water depth (28–29 cm), bottom gravel (3–6 cm), velocity (22–24 cm/sec), and lighting conditions were uniform along the length of the observation flume.

The *light gradient* (Fig. 17,b) was produced with a series of 10 plexiglass sheets. The first sheet was clear, the remaining nine sheets were coated with progressively more black paint. Light intensity in the gradient was measured with a "Photovolt" model 514 M photometer. Table I shows the average light intensity (lux) along the observation flume. Bottom condition, depth, and velocity were the same as in the control.

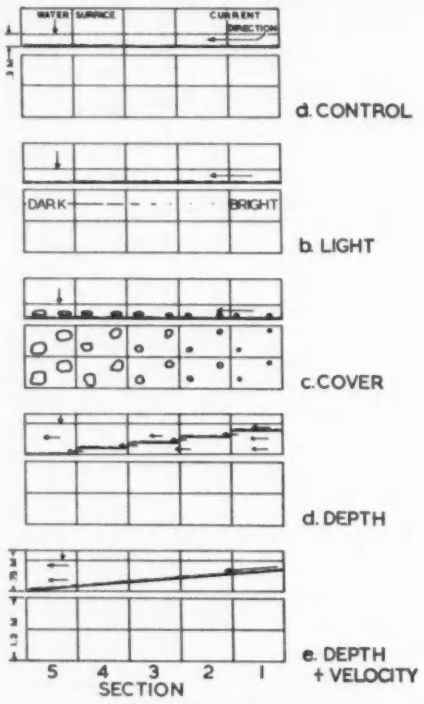


FIG. 17. Lateral and plan views of control arrangement and light, cover, depth, and depth and velocity gradients. Light and control conditions appear similar except for graded filters used to produce light gradient.

TABLE I. Average light intensity over the length of the observation flume. Photo cell readings taken on the bottom with no water in the aquarium.

5		4		3		2		1		Section
4.75	4.25	3.75	3.25	2.75	2.25	1.75	1.25	0.75	0.25	(Meters from upstream end)
2.60	10.8	23.8	48.6	85.3	157.7	189.0	201.9	375.8	281.0	(Lux)[a]

[a]Mean of three readings across the aquarium.

The *cover gradient* consisted of five groups of stones (Fig. 17,c). Stones were elevated above small depressions in the gravel so that each had a 4- to 6-cm cavity under it. The size of stones in each section varied somewhat as given in Table II.

To produce the *depth gradient* four sheets of plywood were arranged stepwise in sections 1, 2, 3, and 4 (Fig. 17,d). Screens between the leading and

TABLE II. Dimensions of stones used in cover gradient.

	Section				
	5	4	3	2	1
Range in:					
Length (*cm*)	22–30	15–17	13–15	10–14	7–12
Width (*cm*)	18–24	12–14	10–11	7–8	5–6
Thickness (*cm*)	4–6	4–7	2–4	2–5	2–4

trailing edges of the steps kept fish above them, but allowed an even flow of water so that velocities were near constant at all depths (Fig. 18). The bottom was covered with the same gravel used in the control. Illumination was slightly higher in the upstream section where the floor panels were elevated closer to the light source.

The *depth-plus-velocity gradient* was produced by means of a sloping false floor (Fig. 17, e). It was not possible to vary velocity along the length of the observation flume without altering depth or width. Details of velocity profiles in horizontal and sagittal planes are shown in Fig. 19. The bottom was covered with the same gravel used in the control. Light intensity on the raised upstream end of the false floor was slightly higher than on the downstream end.

Figure 20 represents the *riffle and pool environment*. This arrangement caused the current to exhibit complex flow patterns which are described briefly below:

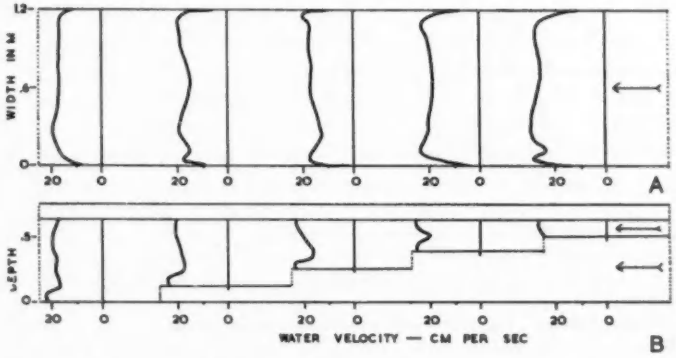


FIG. 18. Velocity profile in horizontal and saggital planes in depth gradient. Upper figure shows velocities 10 cm above bottom, except in section 1, right end, where profile is drawn for position 5 cm above bottom. Lower figure shows conditions in saggital plane (two center readings averaged). Arrows indicate direction of current, dotted lines represent screens.

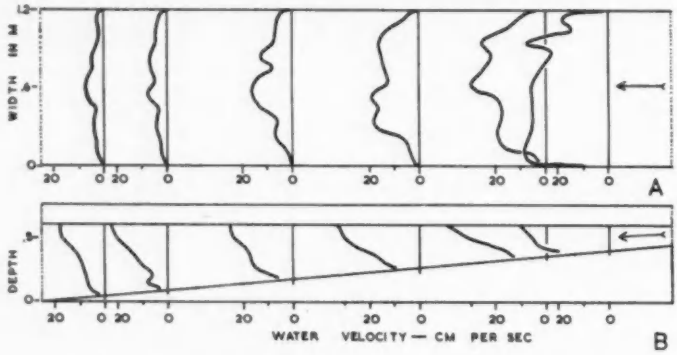


FIG. 19. Velocity profile in depth and velocity gradient. Upper figure shows velocities 10 cm above bottom. Lower shows velocities in saggital plane (two center readings averaged). Arrows indicate direction of flow, dotted lines represent screens.

Pool in section 1, upper 30 cm of water current flows downstream at about 20 cm/sec. In lower 10–12 cm current circulates upstream along the bottom at 4–5 cm/sec.

Pool in section 4, velocity at the surface 28–30 cm/sec, at 20 cm depth about 10 cm/sec and at the bottom, current near 5 cm/sec circulating upstream.

Riffles in sections 2, 3, and 5, current 28–30 cm/sec at the surface and 20 cm/sec along the bottom.

Temperature in the aquarium (Fig. 15) was governed by seasonal changes in the temperature of the water supply, conditions within the building, and energy input from the pump. Tank temperature could usually be lowered by adding fresh water. It could be raised slightly by cutting the input of new water and hence allowing the propeller to heat that already in the aquarium. These measures did not however provide full control. During periods of freshet,

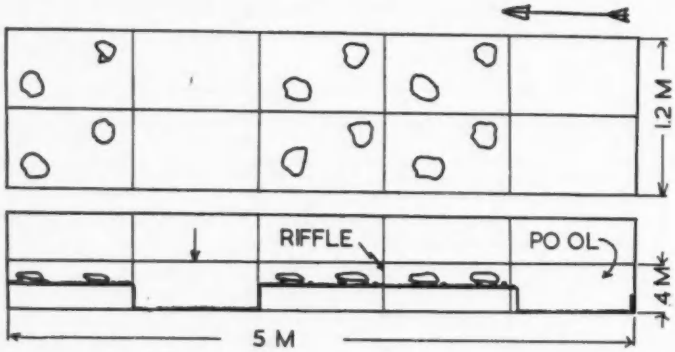


FIG. 20. Horizontal (upper) and lateral views of experimental riffle and pool environment. Horizontal arrow indicates direction of current. Vertical arrow indicates water surface.

the water source became turbid and consequently new water could not be run into the aquarium. If the air temperature in the building was high during such freshets the aquarium temperature rose. If it was low the aquarium temperature fell (see October 5 and 6, November 9, 10, and 11, 1962, and January 8–10, 12–13, 1963, Fig. 15).

Temperatures within the aquarium deviated somewhat from those of the holding troughs early in the winter but approximated them later (Fig. 15). During the spring and summer experiments, water in the stream aquarium ranged from 10 to 16 C and was generally warmer than that in the holding ponds. In the autumn, temperatures in the stream aquarium followed holding trough temperatures and fluctuated from 9.4 to 14.6 C.

Figure 15 shows that stream tank temperatures fluctuated seasonally and daily. They corresponded to those of the holding troughs but were generally higher.

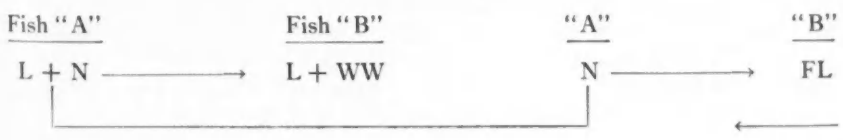
EXPERIMENTAL PROCEDURE

Day length was maintained at 12 hr (0600–1800 hr) in all experiments. This photoperiod was not consistent with that of the holding troughs during the winter. It was necessary however to use a 12-hr day in order to give the fish a 2-hr period of adjustment after the lights came on since the subsequent 10-hr observation period was necessary to obtain adequate records on distribution and behavior.

In all experiments fish were handled, fed, and observed as consistently as possible. In each experiment, 40 fish were placed in still water between 2000 and 2200 hr. At 0800 hr the following day, the current was started at 14 cm/sec and raised in two steps to 23 cm/sec in control, light, and cover gradient. During the first day numbers of fish in each section were recorded at ½- or 1-hr intervals. During the second day positions of all 40 fish were plotted 12–16 times on outline maps of the stream bottom.

Behavior was recorded in a series of 10-min observations along the length of the tank. A preliminary study revealed that the two species exhibited comparable components of agonistic behavior. These were coded so that a sequence of events could be recorded approximately and quantified. The following is a list of behavior elements and their code letters; details of behavior will be described later: L — lateral display, F — frontal display, N — nip, C — chase, WW — wig-wag display, TN — threat nip, IM — intention movement, and Fl — flight.

A protocol for a behavioral sequence is as follows:



In this series of events fish "A" displays in lateral posture then nips "B." Fish "B" displays lateral posture then exhibits a wig-wag display, "A" nips "B" again and "B" flees. The arrow under "FL" indicates the direction of flight.

Fish, fed twice daily in the stream aquarium, were given 8–10 cc of brine shrimp frozen into a block of ice. The food was placed above the screen in the upstream end of the tank where it melted during a period of 20–60 min. Many of the brine shrimp released kept circulating in the current for several hours, thus evoking feeding over a prolonged period. Immediately after feeding fish tended to shift about and temporarily take up new positions. Because of this, observations on behavior were not made until 30 min or more after feeding began.

The procedure followed in studying fish in the riffle-pool arrangement was slightly different from that used with the gradients. Coho and steelhead were studied separately in two series and then observed in combination in a third series. Table III gives numbers and species of fish used and the time schedule followed during the three series of experiments.

To begin each series 20 fish were placed in still water in the aquarium at about 2000 hr. The following day the current was started and increased stepwise to the desired velocity by 0900 hr. On each succeeding day, until the fourth, an additional lot of fish was added at 0800 hr. Feeding and recording of distribution and behavior were as previously described.

Experiments on fish in the riffle-pool arrangement were conducted in July and November 1963 with underyearling fish. Experiments in the control and gradients were done in the spring, fall, and winter. Appendices II–IV give details of gradient experiments.

SCOPE OF THE RESULTS

Experiments were conducted so that seasonal changes in behavior and distribution could be observed in each species and so that differences between

TABLE III. Number and species of fish used in experiments in riffle and pool environment. In Series 1 coho (C) were used alone, in Series 2, steelhead (S) were used alone, and in Series 3 the two species were combined.

	Series 1		Series 2		Series 3	
	No. of		No. of		No. of	
	C	S	C	S	C	S
First day	20	–	–	20	10	10
Second day	40	–	–	40	20	20
Third day	60	–	–	60	30	30
Fourth day	80	–	–	80	40	40

species could be recorded. Seasonal and species comparisons were made on groups of one species of fish at a time. The interaction of the two species was studied in summer and winter conditions in certain experimental arrangements.

Distributional data are based on groups of animals. If individuals had been tested singly, the preferred positions may have been different from those inferred from the distribution of a group. The maximum number at a particular point in a gradient may not always represent the preferred position. In spite of this limitation, however, groups of fish were used because field data are based on the behavior of animals in groups.

Temperatures in the holding troughs and stream aquarium varied at different seasons. These temperatures also fluctuated within each season (Fig. 15). The day length at which fish were held was shorter during winter than during spring and autumn. The effects of variations in these conditions could not be fully evaluated, but physical conditions such as bottom configuration, bottom gravel, depth, water velocity, and light conditions were duplicated in all cases; hence the environment was partially but not fully controlled.

Results

Replication of Experiments

Certain experiments were replicated during the winter and the spring–summer series. Observations on the distribution of coho in the control environment were made twice in April and repeated in June 1963 (Fig. 21). Experiments with each species in the control, the cover gradient, and depth gradient were replicated under winter conditions (Fig. 21 and 22). In general, the duplicate distribution patterns were similar (Fig. 21 and 22). Differences between species were consistent in repeated experiments in the control and cover gradient during the winter series (Fig. 21). Repeated observations in the depth gradient produced similar distribution patterns for each species but the differences between coho and trout in the depth gradient were not consistent (Fig. 22). Although repeated experiments in the depth gradients did not give distributions that were identical, they did reveal that each species exhibited characteristic patterns. In the control and cover gradient, trout were distributed in a skewed "U"-shaped pattern, coho in a sigmoid pattern, usually with highest means in the first two sections of the tank (Fig. 21).

Seasonal Changes in Distribution

Comparison of the data obtained during the three seasonal series of experiments indicates that numbers of fish were more uniform along the length of the tank in spring and summer than in fall or winter (Fig. 21 and 22). The greatest differences in sectional averages occurred in fall or winter. Such large variations in the average number of fish per section were a result of the tendency of many individuals to congregate in one portion of the tank during fall or winter conditions. In spring both species were distributed over the whole bottom area of the aquarium.

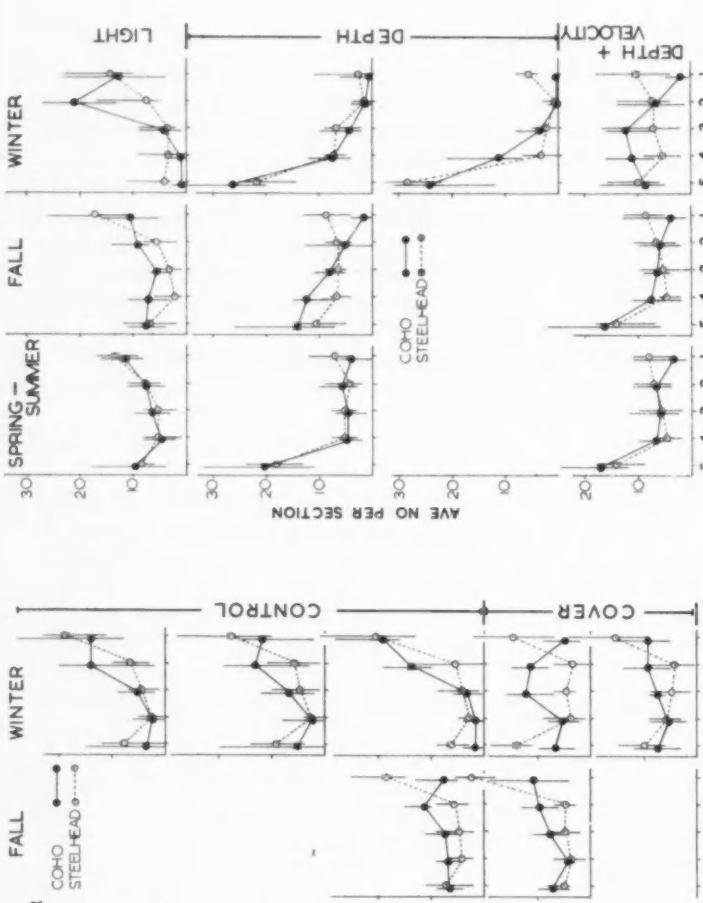


FIG. 21. (*Left*) Distributions of coho and steelhead in "control" and "cover" gradients, described in text, during 3 seasons. Dots and circles represent mean number of fish per section over a 1-day period (10–15 observations). Vertical lines indicate range. Section 1 represents the upstream end of the aquarium.

FIG. 22. (*Right*) Distributions of coho and steelhead in "light," "depth," and "depth and velocity" gradients, as described in text, during 3 seasons. Circles and dots represent mean number of fish per section (10–15 observations). Vertica lines represent range. Section 1 represents the upstream end of the aquarium.

Young coho were scattered in the spring and early summer but in autumn and winter they tended to form aggregates, with some social organization, near the upstream end of the aquarium in the control and the cover and light gradients (Fig. 21 and 22). In the depth gradient the seasonal trend exhibited by coho was a shift to the deepest section of the tank during winter.

In spring and early summer young steelhead were distributed along the tank in a fashion similar to the coho. In fall and winter many trout were active, i.e. moving about in the control, as well as the cover and light gradients (Appendices III and IV). These fish were usually moving and searching about the screen in section 1. The apparent seasonal shift into the upstream region of the aquarium is indicative of wandering and searching in the upstream end, rather than a preference for it. The numbers of stable steelhead positions in the upstream section was usually half, or less, of the numbers shown in Fig. 21 and 22 in the control, depth gradient, and light gradient. Considering this movement, it appears that steelhead which are not roaming assume a more scattered distribution than coho along the tank in the control and the light gradient. Activity accounts for the apparent seasonal shift of fish into section 1 in the cover gradient. However, the high numbers of fish in section 5 represents a preference for positions under or around the large stones. Steelhead, like coho, show a strong winter preference for the deepest section of the depth gradient. Trout exhibited no seasonal change in distribution in the depth-plus-velocity gradient (Fig. 22).

COMPARISON OF SPECIES IN GRADIENTS

In experiments conducted under spring and summer conditions, the distributions of coho and steelhead were similar in each of the five experimental conditions (Fig. 21 and 22). However, in autumn and winter experiments, the distribution differences between the species were greater. Environmental preferences, as inferred from experimental distributions, were most similar in spring and early summer, the season in which segregation was most pronounced in the Salmon River. Distributions and inferred preferences were divergent during fall and winter (Fig. 21 and 22), the seasons in which populations overlapped most in the Salmon River (see Fig. 12). During the season when laboratory distributions are similar the two species meet and interact in the natural stream environment. In the seasons when experimental distributions are different, the two species are most compatible in the natural stream environment. Different environmental responses in the laboratory (i.e. response to cover, Fig. 23, 24) are indicative of the mechanisms that allow the two species to coexist in close proximity in fall and winter.

In the cover and depth gradients young fish utilized stones and pool space in a similar fashion in spring and summer but not in winter. Coho, 6–8 weeks old, scattered among the stones which formed the cover gradation (Fig. 23). During spring about one-third (126 of a total of 412) of the positions taken by coho were immediately downstream from stones. Many positions recorded were among the stones. In winter, 126 of 390 positions occupied

Vertical lines represent range. Section 1 represents the upstream end of the aquarium.

were immediately downstream from the stones. Fish were, however, recorded at fewer positions among the rocks (Fig. 23) in the winter. Those that were not in the shelter of stones were at positions at the sides of the tank.

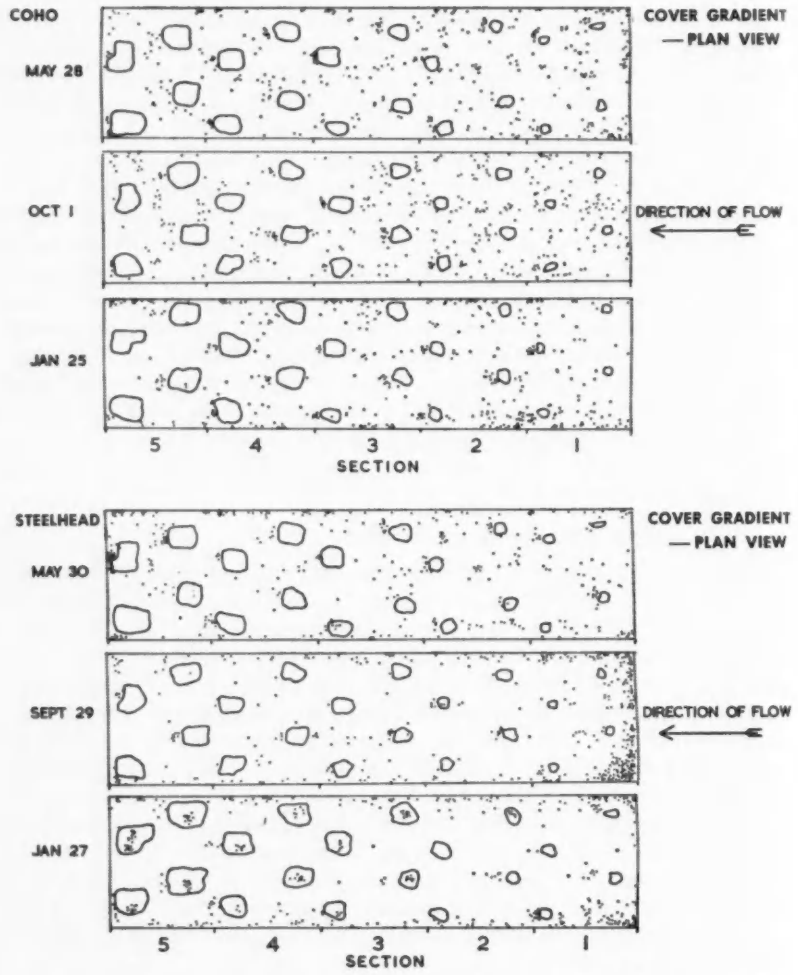


FIG. 23. (*Top*) Distribution of coho in cover gradient during 3 seasons. Locations of 40 fish during 10 combined observations are given. Groups of dots represent same fish occupying same location repeatedly, or different fish in same location repeatedly, in this and succeeding figures of this type. Points within the stone outlines represent fish under stones. Dotted lines represent screens at ends of aquarium in this figure and succeeding figures of this type.

FIG. 24. (*Bottom*) Distribution of steelhead in cover gradient during 3 seasons. Locations of 40 fish during 10 combined observations are given. Points within the stone outlines represent fish under stones.

Steelhead, 3–5 weeks old, distributed themselves in the same pattern as the 6–8-week coho (Fig. 24). During spring, one-third of the steelhead positions were immediately downstream from stones. As in the case of coho, the other positions were scattered among the stones, and none was under them (Fig. 24). During the fall, a large number of young trout was active and remained in the upstream end of the aquarium (Fig. 24). One-sixth of the positions recorded were immediately downstream from stones; only six positions were under them (Fig. 24). In winter one-fourth of the positions recorded were under stones and approximately one-eighth were downstream from them (Fig. 24).

It is evident that the distributions observed in the spring condition would result in a high degree of contact between species if together in a cover gradient. However, in winter the tendency of trout to hide under stones would, to a degree, isolate them from coho which do not do so (Fig. 23 and 24).

A second instance of trout and coho using the same space in a different manner, in winter, occurred in the depth gradient. Table IV shows that in June there is a significant difference in the numbers of young coho and trout in the upper and lower halves of sections 4 and 5 (chi square tests). Segregation is, however, more pronounced during winter. This increase in segregation is primarily due to a change in the behavior of steelhead. In summer conditions, about one-third of the steelhead were off the bottom where they would be in contact with coho if the species were mixed. In the winter most steelhead were spread over the bottom in the deep section. On the other hand most coho were distributed at the edges near the bottom or in loose aggregations up each side of the deepest section. Individuals of both species defended areas along the downstream edge of each depth zone. A large amount of intraspecific fighting occurred in these areas. When the two species were placed together during summer in equal numbers the amount of intraspecific and interspecific aggression was high (Table V). During winter when trout and coho were placed in the depth gradient together they were segregated spatially as already described. Intraspecific and interspecific aggression were lower than under summer conditions (Table V). Interspecific fighting was not disproportionately lower as expected on the basis of spatial segregation. However practically all inter-

TABLE IV. Numbers of coho (C) and steelhead (S) in upper and lower halves of sections 4 and 5 in the depth gradients in early summer and winter (June and January).

	June		January	
	C	S	C	S
Upper half	124	75	168	24
Lower half	103	145	161	281

TABLE V. Aggressive contests per fish per hundred minutes during June and January 1963. Symbols are as follows: C = coho; S = steelhead; C.C = coho attacking coho; C.S = coho attacking steelhead; S.S = steelhead attacking steelhead; and S.C = steelhead attacking coho.

Date	Fish		Number of contests				Observation
	C	S	C.C	C.S	S.S	S.C	
							min
June 28	20	20	12.7	6.1	6.3	1.3	90
January 17	20	20	4.4	1.3	2.4	0.9	90

specific contests occurred at the downstream edges of depth zones in sections 3 and 4. Few aggressive contests were recorded between the coho, in aggregations at the side of the deep section, and trout, on the bottom.

DESCRIPTION OF AGONISTIC BEHAVIOR

Young coho and steelhead display using a number of similar postures and movements. These displays and movements are listed in Materials and Methods. Before any classification and quantification of the behavior components are attempted, it is essential to understand the basis of the classification. Each of the different components appears in a variety of forms which appear to be related to the intensity of the behavior. In the following description of behavior, each component is described and the variability indicated. It is acknowledged that this type of fish behavior could be classified on a more refined scale by quantifying intensity or duration of components. Such was not feasible in this study because of the number of fish that were observed and the rapidity of the action.

Lateral display was described by Fabricius (1953) and Kalleberg (1958). This varied from a simple erection of the dorsal fin, lasting 1 or 2 sec, to a prolonged erection of dorsal and paired fins and a lowering of the basihyal apparatus for 10 or 15 sec. The dorsal line of the body was either straight or slightly recurved. The criterion for a lateral display was the erected dorsal fin and the line of the back. Figure 25,A shows characteristic lateral posture of 10-month-old coho, Fig. 25,B shows lateral posture of 8-month-old trout. Figures 25,C and 26,A illustrate lateral displays in 2-month-old coho. Lateral displays were similar for the two species, although the display was usually more obvious in coho which possess large median fins with long, colored edges (Fig. 25,C and 26,A).

The frontal display, described by Fabricius (1953) and Kalleberg (1958), varied from a posture in which the back was slightly arched, the dorsal fin compressed, and the basihyal extended for 1 or 2 sec (Fig. 25,B and 26,B), to a posture in which the back was strongly arched, the dorsal fully compressed, and the basihyal well extended for longer (unmeasured) periods.

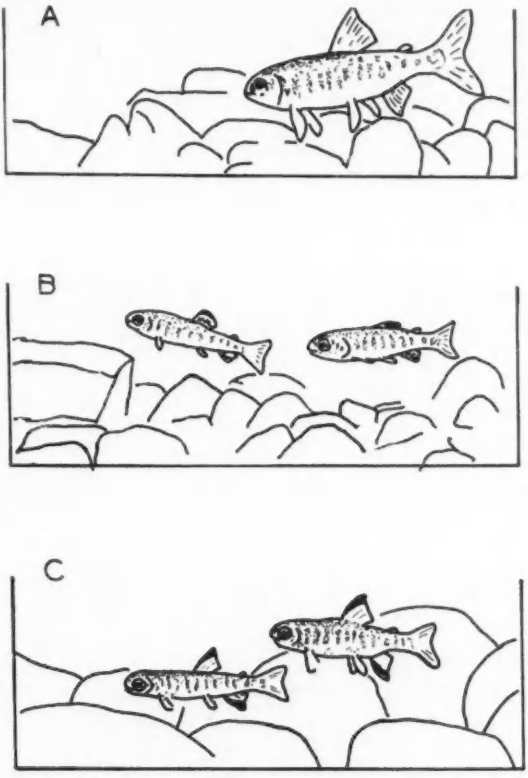


FIG. 25. A. Coho, about 10 months old, in lateral threat posture. B. Steelhead, about 8 months old, in lateral posture (see fish on the left). Fish on the right in frontal threat posture of low intensity. C. Coho about 2 months old, in lateral threat posture. (All figures are traced from photographs.)

In the wig-wag display fish adopted a lateral posture, usually with median and paired fins well extended, and swam with accentuated lateral movements with the head down and the body at a 20–30° angle from horizontal (Fig. 26,B and C). In this display the amount of fin erection varied. The angle of body inclination and the amplitude of swimming movement was low in displays that were of short duration. In wig-wag displays (inferred to be of high intensity) the fins were erected fully, the angle of inclination was steep (near 30°) and lateral movements were accentuated. The criterion for a wig-wag display was the erected fins, the inclined posture, and accentuated swimming movements. As in the case of the lateral display, the wig-wag was more striking in coho than trout because of differences in fin shape and color.

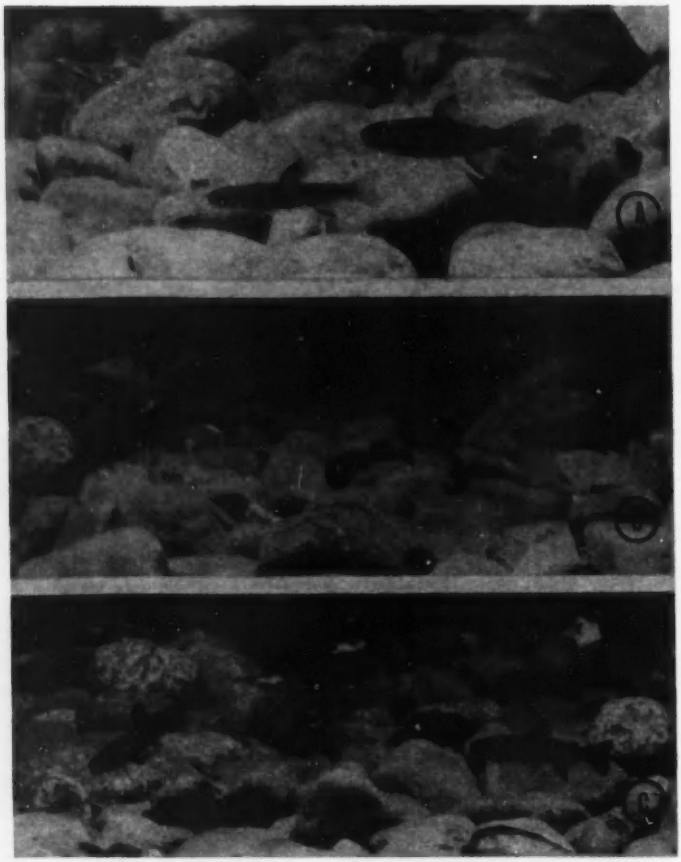


FIG. 26. A. Coho, about 2 months old, in lateral threat posture. B. Coho, about 2 months old, in frontal threat posture of low intensity (right). Coho, about 2 months old, in wig-wag posture (left). C. Coho, about 2 months old, in wig-wag (left) and lateral threat posture (right).

Chasing involved chase and flight. If one fish darted after another and pursued it past the point from which it fled it was designated as chasing. Pursuits ranged from slow short excursions of 20 or 30 cm to long chases of 2 or 3 m.

Nips were those bites in which there appeared to be a definite contact. In some instances fish only "mouthed" the individual attacked. In other cases the bites were so hard that the animals seemed to be briefly stuck together.

Threat nips were nips which were aimed at other fish. Such bites appeared to be inhibited and hence missed contact by as much as 20 or 30 cm. In some cases a fish swam a short distance and nipped in the direction of another.

In other situations they turned their heads and nipped in the direction of a neighbouring fish.

Intention movements were responses in which a fish only turned its head quickly toward another or made a short lunge at it. No threat nip was involved. These movements, which were brief, varied as described and were often difficult to distinguish from nonsocial behavior and threat nips.

An example of an aggressive bout involving several of the described aggressive components was given in the Materials and Methods section. Some contests were short and involved only two or three behavioral components, others were long and involved series of bites and displays interspersed among each other and reciprocated between individuals.

ANALYSIS OF BEHAVIOR

By recording bouts in terms of individual behavior components it was possible to examine the rate of occurrence of various aggressive components as well as complete contests. The breakdown of agonistic behavior into all its components made it possible to compare quality and quantity of aggressiveness in different seasons and species.

Figure 27 represents behavioral repertoires of coho and steelhead during 3 seasons. Details of observation time are given in Table VI. The diagrams in the figure show only the rate of occurrence of each component, they do not show how these may be related to each other during aggression. There are three main points illustrated in Fig. 27. First, the repertoires of the two species differ at all seasons. Second, within each species the amount of aggressive behavior decreases seasonally from spring to winter. Third, the quality of behavior exhibited by each species changes seasonally.

The most obvious species differences were the relatively strong nipping and chasing components of the trout as opposed to strong wig-wag, threat nip, and intention-movement components of coho. The lateral display, which often preceded the wig-wag, was stronger in the coho than in the steelhead during spring and autumn (Fig. 27).

Level of aggressive behavior among coho was high in spring, summer, and fall but decreased during winter. Among trout aggressiveness decreased progressively from spring to autumn and winter.

During spring and winter lateral displays, nipping and chasing were frequent in both species. Nipping and chasing components were very strong in the steelhead (Fig. 27) during spring and summer. Behavior composition of the two species was most similar in the spring; by autumn it had diverged. By winter the lateral display components were greatly reduced and equalled by threat nips and wig-wag elements in the coho. The most evident seasonal change in the steelhead configuration was the reduction of the chase component.

A higher frequency of elaborate displays and noncontact behavior was evident in the coho. The main behavior elements of the trout were lateral displays, biting, and chasing. Hartman (1963) showed that young brown trout (*Salmo trutta* Linn.) displayed frequently, but nipped less at low water velocities (8–9 cm/sec). At higher velocities (18–19 cm/sec and 28–30 cm/sec)

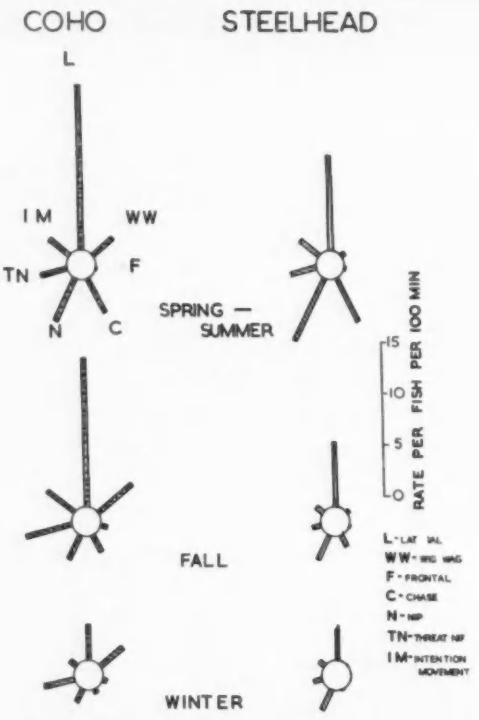


FIG. 27. Rate of occurrence of individual components in the agonistic behavior of young coho and steelhead. Data are based on combined observations of fish in the five experimental arrangements used. See text for description of behavior components.

they nipped relatively more and displayed less. The mechanical difficulty of holding position in the current with median and paired fins extended appeared to be the main reason that agonistic behavior took on a different character at higher water velocities. A comparison of behavior patterns of coho and steel-

TABLE VI. Minutes of observation of coho and steelhead in control and four experimental arrangements during spring, fall, and winter.

Coho	Steelhead	Season
750	410	Spring
390	440	Fall
890	720	Winter

head with brown trout suggests that steelhead behavior, involving primarily lateral displays, nips, and chases, is more adapted to rheocrene conditions than the behavior of coho which involves more wig-wag displays and less nipping. Results of field and laboratory studies also suggest that the differences in behavior of coho and steelhead are related to their ecology.

DISTRIBUTION IN RIFFLES AND POOL HABITAT

The major difference in distribution of trout and coho in the field was related to riffle and pool habitats. In the stream aquarium certain behavior features of each species appeared adaptive to particular current conditions and an attempt was made in the laboratory analyses to determine whether there were behavior characteristics which conferred advantages on trout in riffles and coho in pools.

Distributions in riffle and pool habitats (Fig. 28 and 29) indicate that both species preferred pools or that some environmental regulation of behavior allowed more individuals to remain in the pools. Both trout and coho had similar distributions in the riffle and pool habitats when the species were separate. Steelhead, however, were more numerous in the riffle areas (Fig.

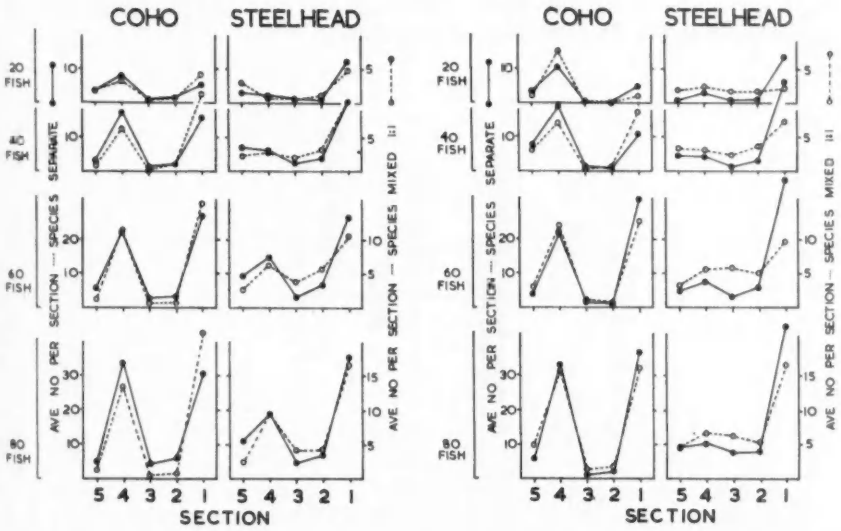


FIG. 28. (*Left*) Distribution of coho and steelhead at four different densities in riffle and pool environment (July). Solid dots represent the average number of fish per section, species separate. Circles and broken lines indicate the average number of fish per section, species mixed. Scale for the points for species mixed is half that for species separate.

FIG. 29. (*Right*) Distribution of coho and steelhead at four different densities in riffle and pool environment (November). Solid dots represent the average number of fish per section, species separate. Circles and broken lines indicate the average number per section, species mixed. Scale for the points for species mixed is half that for species separate.

28 and 29). When coho and steelhead were mixed in July experiments, density of steelhead was reduced (in relation to the situation where the species was alone) in six out of eight cases in the pool habitat, and increased in eight out of 12 instances in the riffle habitat. Coho density was reduced (in relation to the situation where the species was alone) in nine out of 12 cases in the riffles and increased in five out of eight instances in pools. Upon mixing, coho densities increased in the pools and decreased in the riffles, and steelhead densities changed in the opposite direction in more cases than expected by chance ($P < .05$, chi-square test). During winter the effects of interspecific mixing were not clear (Fig. 29). In experiments where the species were mixed, steelhead densities decreased in the pool in section 1, and increased in the three riffle sections in all but one instance. However, density of steelhead in mixed groups was higher in the pool in section 4 also. Changes in relative density of coho showed no consistent relation to those of steelhead as occurred in July (Fig. 28).

AGGRESSIVE BEHAVIOR IN RIFFLES AND POOLS

Levels of aggressiveness were higher in riffle habitat than in the pool habitat when the species were separate (Fig. 30). An exception to this was the case of steelhead under winter conditions. Fighting and displaying occurred more frequently in summer than in winter in the riffle and pool environment as was observed in the experimental gradients.

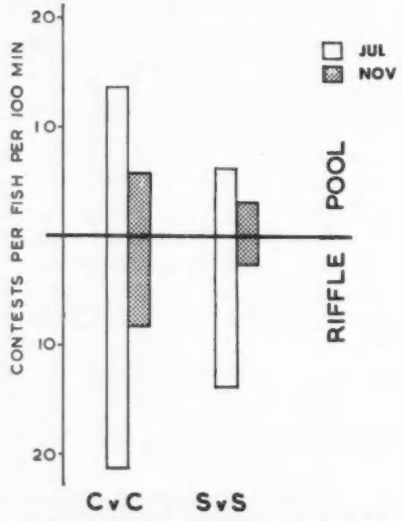


FIG. 30. Rate of aggressive behavior in riffle and pool habitats during July and November. Data based on observations made with species separate. C vs C indicates coho attacking coho and S vs S indicates steelhead attacking steelhead. Coho observed 390 min in July and 340 min in November; steelhead observed 380 min in each period.

Interspecific mixing revealed an environmental effect on behavior which may in a large degree explain why trout maintained themselves in the riffle sections of the aquarium and actually reduced utilization of this space by coho. Figure 31 shows that coho displayed a high level of interspecific and intraspecific aggressiveness within pools. Aggressiveness of trout was correspondingly low in the pools (Fig. 31). (Chi-square values indicate that differences in rates of aggressiveness of trout and coho in riffles and pools during July are significant $P > .01$.) In the riffle habitat of the aquarium coho were not particularly combative; steelhead on the other hand were aggressive (Fig. 31). In addition to being more aggressive, steelhead tended to defend temporary territories. A comparison of Fig. 30 and 31 indicates that mixing the two species in a riffle and pool environment had the effect of reducing the level of coho aggressiveness in riffles and increasing it in pools. The degree of aggressiveness of steelhead in riffles was increased in mixed groups. In mixed groups steelhead fighting was more frequent in the pools in November than in July; such was not the case when the species were separate (Fig. 30 and 31).

High rates of aggressive behavior in the riffles (species unmixed) resulted in low densities of fish in such areas. Behavior differences, which were related

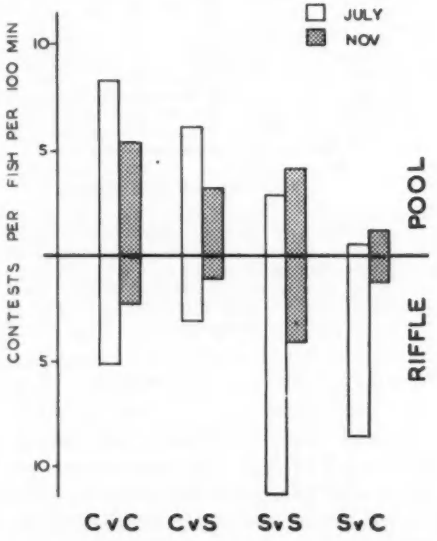


FIG. 31. Rate of aggressive behavior in riffle and pool habitat during July and November. Data based on experiments in which species were mixed in equal numbers and observed 270 min in July and 250 min in November. Meaning of symbols as follows: C vs C = coho attacking coho; C vs S = coho attacking steelhead; S vs S = steelhead attacking steelhead; S vs C = steelhead attacking coho.

to the environment, accounted for the strict density regulation in riffles. Strong current induces more distinct territorial tendencies as has previously been demonstrated (Kalleberg, 1958). In addition the presence of reference objects induces fish to establish and defend territories (Hartman, 1963). In the riffle sections current was fast and there were reference objects, i.e. large stones. Agonistic activities in these areas were easily induced, hence in Fig. 32 rates of aggression were high at low densities. High densities of fish did not occur because increased fighting led to displacement of fish.

In the pools, however, aggression decreased with an increase in fish density (Fig. 32). Keenleyside and Yamamoto (1962) demonstrated almost the

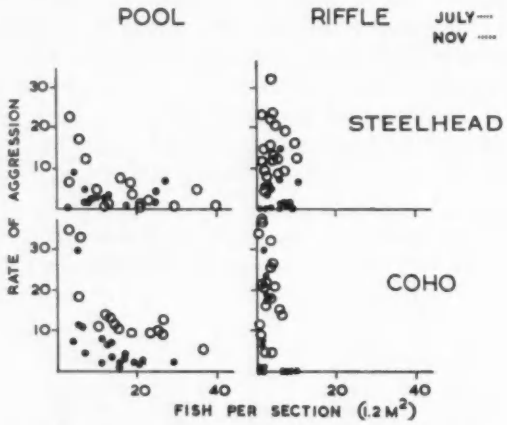


FIG. 32. Relation of rate of aggressive behavior to density of fish. Coho and steelhead compared in riffle and pool habitats during 2 seasons. Each dot or circle represents the number of aggressive contests per fish 100 min during 10 min of observation in one section of the aquarium.

same effect with Atlantic salmon in small still-water aquaria. Reduction in rate of aggression with increase in numbers was particularly evident in coho (Fig. 32). Certain behavior features probably account for this phenomenon in groups of coho. In a group of coho, competition was strongest for positions near the front. In fighting for positions, fish often swam parallel to each other in lateral threat posture. After swimming parallel for a short distance one fish, usually the dominant individual, darted ahead of the second and performed a wig-wag display in which it dropped backward downstream toward the second fish (Fig. 33,A–C). In many cases the upstream fish ended by literally brushing its opponent back with its tail (Fig. 33,C). If the displaced fish remained behind the victor, little more fighting occurred. The wig-wag threat was closely associated with the formation of stable social groups with one to three dominants at the front and several subordinates behind them.

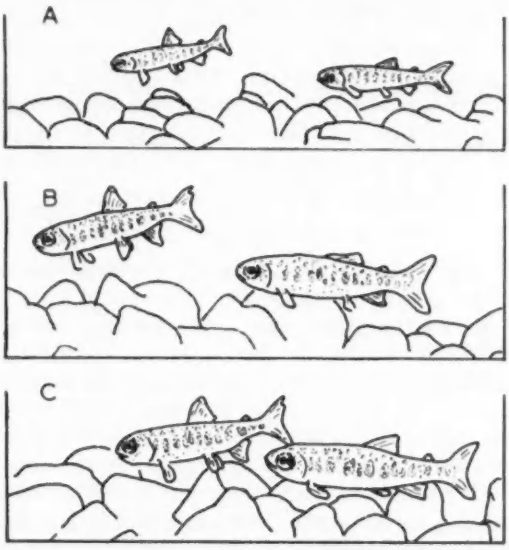


FIG. 33. A. Coho, about 10 months old, in wig-wag posture. Fish at left is displaying and beginning to drop back toward fish at right. B. Both fish dropping downstream and coming closer together. C. Coho at left still in wig-wag posture, its tail almost striking fish at right. At this point the fish at left may wheel and nip the second fish or second fish may flee.

Steelhead did not establish stable social groups as did coho. In July observations, aggressiveness decreased with increase in numbers of steelhead. Such a change took place because as numbers went up many steelhead settled to the bottom and became quiet while others began to roam about. These fish were not often attacked. There were usually large, potentially dominant trout; they did not often exhibit the wig-wag threat and did not hold the front positions in any stable groups.

SUMMARY OF RESULTS

Field observations revealed seasonal changes in the distributional relationships of young coho and trout. Concomitant with these were changes in water temperature, and population density. Laboratory experiments pointed to features of environmental and social behavior which were related to changes occurring in nature. Field and laboratory results are summarized below as an introduction to the Discussion. Field observations apply particularly to the Salmon River.

SPRING AND EARLY SUMMER

Field observations	*Laboratory observations*
1. Species largely segregated in different microhabitats.	1. Both species have similar distributions in experimental gradients.
2. Coho in pools, trout in riffles.	2. Both utilize space in pools and cover in the same manner.
3. Population density per unit of area is high.	3. Both species exhibit high level of aggression which involves much biting and chasing.
4. Coho relatively large compared to trout.	4. Coho larger than trout.
5. Temperature of water 8.3–17.2 C (time corresponds to laboratory period).	5. Temperature 10–16 C.
6. Body and fin colors vivid.	6. Body and fin colors vivid.

FALL

Field observations	*Laboratory observations*
1. Species partially segregated in early fall, coming together more in late fall.	1. Steelhead and coho have different distributions in experimental gradients.
2. Coho in pools, trout density about even in riffles and pools.	2. Species utilize space and cover in about the same manner.
3. Population reduced in pools, reduced more in riffles.	3. Coho aggression high, but less biting and chasing is exhibited. Steelhead aggression lower than in spring, relatively less chasing.
4. Trout size range approximating that of coho.	4. Temperature 9–14.5 C.
5. Temperature of water 7.2–12.5 C.	5. Body and fin colors less vivid.

WINTER

Field observations	*Laboratory observations*
1. Species exhibit no microhabitat segregation.	1. Species have different distributions in experimental gradients.
2. Highest density of both species in the pools.	2. They utilize space in pools and around cover in different manners.
3. Population density reduced further in pools, very low in riffles.	3. Aggression very low in both species. Coho display components are strong, very little biting and chasing. Steelhead show only two components strongly: simple displays and biting.
4. Trout size range approximating that of cohos.	4. Temperature 0.5–7.5 C.
5. Temperature of water 0.3–7 C.	5. Body and fin colors less vivid than in spring and fall.

DISCUSSION

An animal's behavior is adapted to its environment, as is its morphology and physiology. Accordingly, there are both environmental and social responses of coho and trout which relate to their ecology. Certain aspects of the ecology and behavior of coho and trout will be considered before entering the main body of the discussion, which will deal more directly with interspecific interaction.

BEHAVIOR OF STEELHEAD AND COHO IN RELATION TO THEIR ECOLOGY

Under natural conditions coho were most frequently distributed in groups which were restricted to certain types of habitat. Trout were more scattered and appeared capable of utilizing a wider array of stream habitats. Under experimental conditions coho were best adapted to maintaining positions in pools, and trout to holding positions in riffles. These differences, which are most evident during spring and summer, probably account for differences in population stability of the two species in small coastal streams. During May and June large numbers of young coho were displaced downstream in the Salmon River. Chapman (1962) has shown that such displacement is the result of aggression and competition for space. The emigration of young coho from streams occurred at a season when levels of aggression were highest and when behavior was least ritualized.

Downstream displacement of trout did not occur even though density and rate of aggression were high. Kalleberg (1958) showed that territory size decreased with increased population density of Atlantic salmon fry. Trout in the Salmon River may accommodate for changes in numbers by changing territory size. Coho, which are restricted to pools, may displace surplus individuals out of the pools. Experimental data indicated that such individuals would be unable to maintain positions against trout in the riffles. As a result coho, pushed out of pools, would move downstream to unused pool space or be displaced completely. The direction of retreat following combat may be important in a consideration of the matter of downstream displacement. Retreating trout in the experimental stream aquarium tended to move upstream or laterally. Figure 34 shows that about 25% of the coho retreats were lateral and 30% were upstream. However, the largest single percentage (about 45) of retreats was downstream. These differences are consistent with differences in amount of downstream displacement and with the type of aggressive behavior exhibited by coho and trout.

During winter, coho are usually found in dense groups. The tendency to form such groups is usually reflected in the winter distributions (Fig. 21 and 22). In winter no downstream emigration occurred in the Salmon River. Laboratory studies revealed several behavioral phenomena which would facilitate stability of groups in restricted areas of the stream during the winter. Levels of aggressiveness were lower in both species. The amount of biting and chasing was low in proportion to noncontact aggressiveness. The wigwag display occurred frequently in laboratory conditions and was exhibited

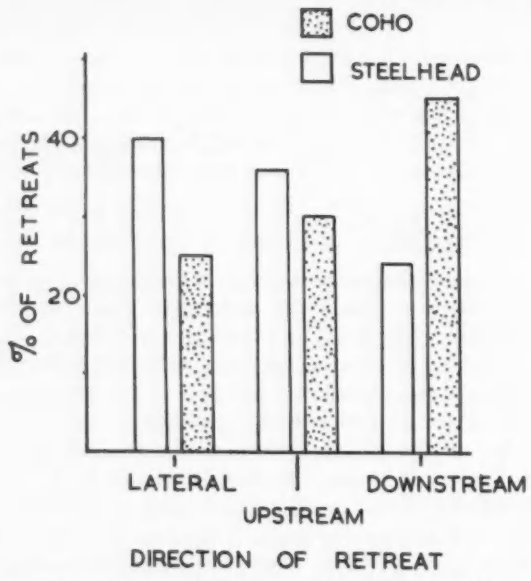


FIG. 34. Direction of retreat of coho and steelhead following intraspecific aggressive contests (based on 248 contests among steelhead and 458 among coho).

in contests for position near the front of a group. Fish which were displaced by others using the wig-wag threat were pushed back into the group of subordinates but were not driven entirely out of the group.

During winter, trout did not occur in tight groups as did coho. Behavior components (threat nips and wig-wag displays) which were evident in the group behavior of coho were exhibited infrequently in laboratory groups of trout.

Hiding behavior shown by trout under winter conditions has adaptive value in protecting them from "scouring" and predation. Coastal rivers of British Columbia are frequently subject to freshets, hence, hiding behavior, either in log jams or under stones, is advantageous in maintaining position. Lindroth (1955b) has shown that mergansers can take a heavy toll on trout parr populations. Lindroth and Bergström (1959) demonstrated that mergansers could easily see fish in open water and chase them tenaciously. The birds even searched actively under the stones for the trout parr. It may be assumed that fish in positions under large stones would gain considerable protection from such predation. In most cases hiding trout in the Chilliwack River were under rocks 20–40 cm in diameter. Many hiding fish were found well down among the stones rather than near the surface. The habit of seeking shelter is important in the ecology of young steelhead because it offers protection from winter freshets and from predation to many fish which are distributed along the stream margins in otherwise unprotected locations.

The foregoing comments have pointed out some differences in the behavior and ecology of the two species. Although trout occupy a wider variety of stream habitats than coho (particularly in the largest stream) the two species overlap to a large degree in space utilization.

INTERACTION OF YOUNG STEELHEAD AND COHO

Segregation of natural populations of young coho and trout occurred at the season in which experiments indicated great similarity of environmental preferences. Separation in the wild was least pronounced during winter months, when experiments indicated differences in preferences. These two observations considered together support the belief that interspecific competition may be manifested in segregated resource use as suggested by Nilsson (1956, 1963). Interaction, which occurred in spring and summer because both species had similar demands, was accentuated by three factors. Population densities (in the stream) were highest in spring and summer (Fig. 12). Levels of aggressiveness (laboratory) were highest early in the year (Fig. 27). In addition to this the aggressiveness shown involved much biting and chasing. Size differences may have contributed to the effect of segregation. Coho in the Salmon River were larger than the trout in spring and summer (Fig. 13) and could have displaced them from pools.

In direct opposition to the above situation, winter populations of coho and trout coexisted to a large extent in the pools. Three main factors contributed to this interspecific compatibility. First, spatial distribution and preferences of the two species in the stream aquarium were different in winter. Second, stream population densities were lower in winter (Fig. 12). Third, levels of aggressiveness were lower in winter (Fig. 27). These three factors must contribute substantially to the winter coexistence of coho and trout.

There is an apparent paradox in the fact that wild populations of both trout and coho occupy pools at a season when experiments indicate differences in preferences. It should be pointed out, therefore, that both species showed a preference for the deepest section of the depth gradient, which was comparable to a pool (Fig. 22). However, trout and coho utilized this pool space differently; coho formed groups in open water above bottom, and trout scattered across the bottom. In the cover gradient trout occupied space under stones but coho occupied space beside the stones or downstream from them (Fig. 23 and 24). In a stream during the winter both species may make a demand on pool space. However, small but important differences in the use of space and cover, such as those described, permit coexistence of both species in a pool within a few inches of each other. As already stated, such coexistence would be facilitated because levels of aggressiveness in both species are low during winter.

The previous discussion explains some of the reasons why coho and trout segregate spatially in spring and summer but occur together in winter. However one important question still remains. How do these two species remain in equilibrium in the two distinctive natural microhabitats, riffles, and pools?

To gain better understanding of this problem it may be valuable to consider the effect of environment on the behavior of young brown trout. Hartman (1963) showed that young brown trout could be induced to take up and defend positions if presented with simple visual reference points. If the structural complexity of these reference points was increased, the rate of occupancy was increased. Kalleberg (1958) showed that defence of territories by young brown trout and salmon was initiated by running water. Territorial behavior of young brown trout was released by certain stimuli, the effect of which could be reinforced by others. The behavior of choosing and defending territories appears to be a reactive type of behavior which is governed by a complex of environmental stimuli. Presumably young steelhead in the riffle environment received more stimuli which elicited aggressive behavior and territory defence, than they received in the pools. The responses of young coho to various stimuli were different, hence, they were more strongly motivated to defend space in pools and less so in riffles. Such a differential response to environmental conditions is indicated by the differences in aggressiveness in riffle and pool habitats (Fig. 31). Segregation in the Salmon River is probably maintained because of differences in motivational states of trout and coho in the three microhabitats of the stream. If it were not for this differential aggressiveness, coho displaced from pools would be able to eliminate the smaller trout from the riffles, thus shifting the balance, in the whole stream, in favor of one species.

In concluding the comments on the ecological relationship of these two species it is emphasized that changes in social behavior account, in a large way, for the seasonal change in severity of interaction. Differences in aggressiveness in riffle and pool environments account for the segregation and the equilibrium of coho and trout in the two microhabitats.

COMMENTS ON CONCEPTS OF COMPETITION

A number of investigators have reported instances in which competition or interaction between species is manifested in segregation (Beauchamp and Ullyott, 1932; Macan, 1961; Connell, 1961). Segregation produced by competition among fish has been recorded by Nilsson (1955, 1958, 1960, 1963). Miura (1962) reviewed several cases in which it occurred in competing species of Japanese fish. Lindroth (1955), Kalleberg (1958), and Saunders and Gee (1964) deal with segregation of competing species of stream-dwelling salmonids. In most of the preceding cases each species has a slight morphological, physiological, or behavioral advantage over the other in some part of the environment. It is considered necessary to emphasize that similar, competing species segregate and come into equilibrium in nature since many laboratory investigations on competition, carried out in homogeneous controlled environments, would indicate otherwise (reviews by Crombie, 1947; DeBach and Sundby, 1963). Grinnell (1904), Gause (1934), and DeBach and Sundby (1963) have indicated that species having the same niche cannot occur together without one eliminating the other. DeBach and Sundby (1963) have

recorded a case in which one species of *Aphytis* eliminates another and is subsequently displaced by a third species. They suggest that the displacement mentioned above illustrates "the competitive displacement hypothesis," i.e. species with identical ecological niches cannot coexist long in the same habitat. Because of the way the hypothesis has been stated and because of the variations in its interpretation, the competitive displacement concept has been controversial (Hardin, 1960; Cole, 1960; Patten, 1961; Van Valen, 1960; McIntosh, 1961). The concept might have been more acceptable if it had stated that in sympatric populations of similar species the level of competitive interaction will increase with the degree of ecological and behavioral similarity. This does not lead to the difficulty of discussing different species with *identical* niches, although it does still leave the problem of quantifying ecological and behavioral similarity. It is impossible to say how such interaction will be manifest, because competition in the natural environment may alter the numbers, the growth rate, or the niche of an animal in a particular habitat. Temperate freshwater fish are in general unspecialized and flexible (Larkin, 1956) and hence can alter their niche, as young trout and coho are presumed to do. This, on the other hand, may not be true of fish in the old freshwater environments studied by Fryer (1959).

Highly specialized animals such as the parasitic wasps (DeBach and Sundby, 1963) may be virtually incapable of occupying an altered niche; thus elimination of one species is the necessary outcome of competition when no additional factors control the numbers of both competing species. It is reasonable to assume that the amount of specialization as well as the degree of similarity of species will determine the effects of competition. These effects may involve displacement in space, displacement or segregation in food habits, separation in some gradient of environmental conditions, changes in growth rates, or the complete elimination of one species. Species interaction need not be manifested in one type of end result only.

In the field of ecology, hypotheses can be postulated more easily than they can be tested. The present research adds support for the concepts advanced by Nilsson (1956, 1963). In doing so it has emphasized the role of behavior in the interaction of species and has shown how animal behavior may enter into certain problems in population biology.

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APPENDIX I. Mean fork length and range of samples of fish used in experiments, October 30, 1962, to November 23, 1963.

Date preserved or measured	Period when used	Species[a]	Mean fork length	Range	Sample size
			mm	*mm*	
Oct. 19–20, 1962	Nov. 1, 1962 to Feb. 20, 1963	C	58.3	40–95	13[b]
		S	50.9	38–72	20[b]
Jan. 10, 1963	"	C	68.6	52–97	73
	"	S	60.7	50–75	40
Jan. 19, 1963	"	C	66.2	47–88	40
	"	S	61.7	47–76	40
Apr. 25, 1963	"	C	67.5	51–99	56[b]
	"	S	59.3	49–67	40[b]
May 1, 1963	May 7 to	C	37.9	35–42	15[b]
May 25, 1963	Nov. 23, 1963	S	33.5	26–42	22[b]
June 8, 1963	"	C	43.4	40–47	16[b]
June 12, 1963	"	S	39.7	29–49	62[b]
July 19, 1963	"	C	52.1	38–64	65
"	"	S	42.7	35–56	64
Sept. 2, 1963	"	C	66.4	50–89	60
"	"	S	56.2	39–80	74
Oct. 8, 1963	"	C	73.1	52–104	65
"	"	S	72.7	54–102	36
Nov. 23, 1963	"	C	76.7	62–93	30[b]
"	"	S	73.2	47–112	35[b]

[a]C = coho; S = steelhead.
[b]Measurements made on preserved material.

APPENDIX II. Details of spring and early summer experiments comparing behavior and distribution of coho and steelhead.

Date and year	Arrangement in aquarium	Species (40 fish)	Temperature range (C)	Day length in holding pond	Average number moving
1963					
April 19–21	Control	Coho	6.5–8.3	12	1.8
" 21–23	"	"	8.5–9.2	12	2.7
June 7–9	"	"	11.7–12.0	12	3.9
" 9–11	"	Steelhead	14.0–14.3	12	6.0
May 26–28	Cover	Coho	10.0–11.2	12	3.7
" 28–30	"	Steelhead	13.0–13.3	12	2.2
June 11–13	Light	Coho	13.0–13.5	12	4.1
" 13–15	"	Steelhead	13.4–14.0	12	1.9
June 22–24	Depth	Steelhead	15.2–15.6	12	4.8
" 24–26	"	Coho	14.0–15.9	12	4.1
June 30–July 2	Depth and velocity	Steelhead	14.0–14.5	12	9.8
July 2–4	" "	Coho	14.9–15.4	12	8.4
April 28–30	Cover	"	7.1–7.5	12	2.5
" 24–26	"	"	7.1–8.4	12	1.1
June 16–18	Depth	"	15.0–16.0	12	3.5

APPENDIX III. Details of fall experiments comparing behavior and distribution of young steelhead and coho.

Date and year	Arrangement in aquarium	Species (40 fish)	Temperature range (C)	Day length in holding pond	Average number moving
1963					
Sept. 19–21	Control	Steelhead	12.7–13.3	12	7.9
" 21–23	"	Coho	13.2–13.4	12	3.0
" 27–29	Cover	Steelhead	12.3–13.1	12	11.5
" 29–Oct. 1	"	Coho	14.2–14.5	12	2.6
" 23–25	Light	"	12.7–13.5	12	3.5
" 25–27	"	Steelhead	13.6–14.2	12	11.6
Oct. 1–3	Depth	Coho	12.5–13.0	12	3.9
" 3–5	"	Steelhead	11.6–12.1	12	7.2
" 5–7	Depth and velocity	Coho	10.1–10.6	12	6.2
" 7–9	" "	Steelhead	10.8–11.0	12	7.5

APPENDIX IV. Details of winter experiments comparing distribution and behavior of young steelhead and coho.

Date and year	Arrangement in aquarium	Species (40 fish)	Temperature range (C)	Day length in holding pond	Average number moving
1962–63					
Nov. 5–7	Control	Coho	6.9–7.1	12	8.7
" 19–21	"	"	7.2–7.8	9	6.3
Dec. 4–6	"	"	4.7–4.9	8	—
Nov. 11–13	"	Steelhead	7.0–7.1	12	18.3
" 17–19	"	"	6.2–7.2	12	17.7
Dec. 6–8	"	"	5.2–5.7	8	19.7
Nov. 30–Dec. 2	Light	Coho	2.7–3.2	9	2.2
Dec. 2–4	"	Steelhead	3.1–4.0	9	7.4
" 17–19	Depth and velocity	Coho	5.0–5.3	8	5.0
" 19–21	"	Steelhead	5.3–5.6	8	10.6
Jan. 19–21	Cover	Coho	2.0–2.4	8	1.1
" 23–25	"	"	2.4–2.8	8	2.1
" 21–23	"	Steelhead	3.0–3.1	8	7.0
" 25–27	"	"	2.8–2.8	8	8.1
" 8–10	Depth	Coho	1.7–2.5	8	2.3
" 12–14	"	"	0.5–1.0	8	0.6
" 6–8	"	Steelhead	3.9–4.4	8	0.7
" 10–12	"	"	0.8–1.0	8	0.9

Carbon Balance Experiments with Marine Phytoplankton[1,2]

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ABSTRACT

Carbon budgets were prepared for eight species of marine phytoplankton organisms in culture and one natural red tide population during 5-hr experiments at 21 C and light intensity 0.07 cal/cm²/min. Net cell carbon increase, dissolved organic carbon excretion, and respiration were each determined by two or more independent methods.

In diatoms, net oxygen production gave higher estimates of carbon assimilation than did direct carbon measurements, which were not accounted for by excretion of dissolved organic matter. Carbon-14 assimilation agreed well with the increase in oxidizable particulate carbon and with decrease in dissolved CO_2 of the medium, the latter after correcting for excreted organic carbon.

Dunaliella tertiolecta excreted a constant fraction of its assimilated carbon regardless of its physiological activity. In diatoms excretion increased as cells became physiologically inactive.

Thalassiosira rotula excreted similar amounts of carbon in light and dark. In two other diatoms excretion increased on darkening. In these short-term experiments carbon-14 sometimes gave low estimates of excretion by diatoms probably because both labelled and nonradioactive compounds were released by the cells.

INTRODUCTION

We have attempted to measure separately three components of gross photosynthesis in phytoplankton cultures: (1) inorganic carbon assimilated and retained by cells, (2) carbon assimilated and then lost into the medium as soluble organic compounds during the experiments, and (3) CO_2 release in cellular respiration. We refer to the first component as "net assimilation," to the second, regardless of mechanism, as "excretion," and to the third as "respiration." The experiments typically employed axenic cultures, with exceptions being a uni-algal but nonaxenic culture of *Thalassiosira rotula* and a local "red tide" dinoflagellate population. Population density was high in each experiment by sea standards, but not so dense as local dinoflagellate blooms.

The experiments were undertaken partly to seek further documentation of excretion and partly to determine if excretion is the explanation for large differences apparent in primary productivity as measured by the oxygen and carbon-14 techniques. Several investigators of primary productivity of coastal diatom populations (Miyake *et al.*, 1954; McAllister *et al.*, 1961; Antia *et al.*, 1963) record estimates of photosynthesis by the oxygen method significantly

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higher than that given by the carbon-14 method after allowing for a photosynthetic quotient (O_2 production/CO_2 consumption) of 1.25 as recommended by Ryther (1956) and Strickland (1960). Laboratory experiments (Ryther, 1956; Thomas, 1964), however, gave similar results with both methods when applied to *Dunaliella* spp.

The parameters we selected to estimate the three components of gross photosynthesis were: (1) *net assimilation:* a) carbon-14 retained by the cells, b) increase in particulate organic carbon, c) increase in cell numbers and photosynthetic pigments, d) net oxygen production; (2) *excretion:* a) carbon-14 remaining in the medium after acidifying and bubbling with air, b) increase in dissolved, oxidizable organic carbon; (3) *respiration:* a) decrease in dissolved oxygen of the medium, b) rate of loss of cell carbon-14 in the dark immediately following illumination, c) decrease in particulate organic carbon in the dark. In addition, the decline in dissolved CO_2 gave a measure of net assimilation plus excretion. Thus net assimilation, excretion, and respiration were estimated independently by at least two techniques, allowing cross-checks on the accuracy of each measurement. To allow quantitative comparisons between experiments to be made, we maintained the cultures at one temperature and one light intensity.

McAllister *et al.* (1964) recently published the results of similar experiments with the added feature of exposing cells to several light intensities. Their experiments were not intended to establish precise carbon budgets and lack some of the analyses included in this study, especially a direct measurement of excretion. However, it is the only previous study in our acquaintance from which a carbon balance for phytoplankton can be computed. We have improved upon it, at least for the present purpose, by adding direct estimates of excretion, the determination of CO_2 decrease in the medium, and by including more species. Some measurements of cell volume and composition in relation to growth, carried out during the culturing phase, will be published separately in a different context.

METHODS

Species of Phytoplankton and Sources of Cultures

CHLOROPHYTA

Dunaliella tertiolecta Butcher. Clone from Haskins Laboratory.

PYRROPHYTA

Peridinium trochoideum (Stein) Lemm. Clone from Haskins Laboratory.

A natural "Red Tide" population consisting primarily of *Cochlodinium* sp. and *Gymnodinium* sp.

CHRYSOPHYTA

Coccolithus huxleyi (Lohm) Kampton. Woods Hole Oceanographic Institution clone BT-6.

Syracosphaera (Hymenomonas) *elongata* Droop. Clone from Haskins Laboratory, Droop No. 62.

BACILLARIOPHYTA

Ditylum brightwellii (West) Grunow. Clone from T. Smayda, University of Rhode Island.

Thalassiosira rotula Meunier. Clone from T. Smayda, U.R.I. (not axenic).

Cyclotella nana Hustedt. WHOI 13-1.

Skeletonema costatum (Greville) Cleve. Clone from Haskins Laboratory.

Culture Media

Local sea water taken 1–2 miles offshore and supplemented with KNO_3 or NH_4Cl at 500μM, K_2HPO_4 at 50μM, trace metals as in ASP-2 (Provasoli *et al.*, 1957), Na_2SiO_3 at 250μM for diatoms only, and vitamins thiamine, cobaltamin, and biotin at 200, 1.0, and 1.0 μg/litre, respectively, served as culture medium. The media were sterilized by filtration through membrane filters of 0.22 μ pore size, inoculated and transferred to a pair of 5-litre diphtheria toxin bottles for incubation.

Culture and Experimental Conditions

The culture bottles were maintained at 21 C and 0.07 cal/cm^2/min light intensity in an incubator described by McAllister *et al.* (1964). The light, from G.E. T3Q iodine vapor tungsten lamps, 500-w, passed through flowing cold water and a chemical filter (Jitts *et al.*, 1964) to simulate submarine light. Sterile air was bubbled through the cultures for mixing and to supply CO_2. We made occasional sterility checks in the culturing period but found evidence of bacteria only with *Thalassiosira rotula*.

To prepare for the experiments we incubated cultures until a sufficient population density was reached to allow suitable precision of the analytical methods (Table I). The culture was then subdivided into 300-ml BOD bottles and incubated for a further 5-hr experimental period under the same conditions of light and temperature as in the culturing phase. In some of the experiments bottles were returned to the dark at the end of the 5-hr experimental period for subsequent sampling.

Analytical Measurements

The following methods are described in detail by Strickland and Parsons (1965) along with estimates of precision: dissolved oxygen by the Winkler method; phytoplankton pigments; particulate oxidizable organic carbon; uptake of radioactive carbon; dissolved CO_2 by van Slyke manometry. We used a Coulter Counter, Model A, to obtain cell numbers. Carbon 14 in ampules, standardized by scintillation counting by Dr H. R. Jitts, were checked with

TABLE I. Miscellaneous data at the beginning of the carbon balance experiments.

Experiment	Cell number (cells/litre $\times 10^{-6}$)	Cell carbon (mg/litre)	Chlorophyll *a* µg/litre	pH	Comment
Dunaliella tertiolecta					
1	160	–	59	8.48	
2	185	–	169	7.8	pH adjusted with CO_2 gas. Culture diluted from 230 $\times$ 10^6 cells/litre.
3	125	4.92	120	8.4	
4	133	6.17	120	–	
5	223	–	154	8.40	
Skeletonema costatum					
1	104	2.26	42.2	8.3	
2	420	6.87	211	7.6	pH adjusted
3	337	11.3	161	8.64	
4	206	6.7	78.7	–	
Ditylum brightwellii					
1	23.6	19.2	319	7.98	pH adjusted
2	7.47	6.80	119	7.82	pH adjusted
Thalassiosira rotula	26.3	7.61	162	8.48	
Cyclotella nana	104.7	4.27	40.7	8.25	
Red tide					
1	10.4	17.1	278	8.50	
2	6.80	12.3	150	8.50	
Peridinium trochoideum	7.80	9.95	43.7	8.3	
Coccolithus huxleyi	1,500	6.43	60.8	8.35	
Syracosphaera elongata	34.9	9.4	210	8.5	

a Nuclear-Chicago Dynacon counting system. The gas-flow G-M counter efficiency was determined by counting samples and then wet-oxidizing them and finding the activity of the resulting CO_2 with the Dynacon system. Coccolith C^{14} was measured by Paasche's technique (1963). Organic carbon-14 in culture media, after removing cells, was estimated by first acidifying to pH 3 with HCl, allowing air to bubble through for 5 min to remove radioactive CO_2, then bringing the pH to 10 with NaOH. Aliquots were then transferred to

planchets and dried slowly under an infrared lamp. A radioactive glucose solution in sea water, treated in the same way, served as a standard. Light intensity was measured using a Weston photronic cell calibrated against a thermopile radiometer.

At least four sources of variability were noted in experimental manipulation: (1) due to cells settling and sticking the experimental bottles may differ slightly in cell number; (2) variations in the light field in the incubator result in each experimental bottle receiving a slightly different light flux; (3) although the bottles were rotated frequently we noted some settling resulting in mutual shading (pigment content is especially sensitive to this sort of variability); (4) time differences in sampling for the different analyses could lead to variability between methods (we sampled in order of decreasing precision of the methods).

RESULTS

Net Carbon Assimilation

A summary of results is given in Table II including estimates from cell carbon increase, carbon-14 uptake, decrease in dissolved CO_2, increase in cell number, and oxygen production. Median values for excretion are subtracted from the estimates based on dissolved CO_2 decrease and oxygen production to give values comparable to the other estimates. The agreement between the first three estimates is quite satisfactory. Estimates of net assimilation by oxygen production are satisfactory only for *Dunaliella tertiolecta* experiments 3 and 4, the second red tide, *Peridinium trochoideum*, *Cyclotella nana*, and *Coccolithus huxleyi* experiments. High values, exceeding the inherent error of the method, are found in all the other experiments.

To gain perspective we calculated the experimental photosynthetic quotients (PQ). The PQs are variable for *Dunaliella;* 1.1–1.2 for *Peridinium* and *Coccolithus*, as expected; about 0.9 for natural red tide populations which contained animals and heterotrophs, as noted earlier by Sargent and Hindman (1943); and about 1.6 for diatoms. From the composition of diatoms (Parsons *et al.*, 1961) we estimate a PQ of only about 1.3. Because the PQ is related to the form of nitrogen supplied in the culture medium (Cramer and Myers, 1948; Myers and Cramer, 1948) we grew *Skeletonema* with NH_4Cl instead of KNO_3 and found the PQ to be only about 0.2 lower than with NO_3.

Net assimilation in these experiments, as in others, follows closely the chlorophyll *a* content of the cell suspension. The mean ratio of net milligrams of carbon assimilated/milligrams of chlorophyll *a*-hour is 2.8. This value is in the lower range of values found in the literature (Strickland, 1960) due to inclusion of two values (*Skeletonema* experiment 3, *Ditylum* experiment 1) from cultures approaching stationary growth and presumably due to the incident light intensity being less than saturating for some species.

Excretion

Results are summarized in Table III. Estimates of excretion from the difference between O_2 production and net assimilation seem high and are

TABLE II. Summary of net carbon assimilation data.

	Changes of carbon concentration (mg C/litre, during each 5-hr experiment)						
	(1)	(2)	(3)	(4)	(5)	(6)	(7)
Experiment/Method	Cell carbon	C^{14} (cells)	Dissolved CO_2[a]	Mean net C-assimilation[b]	Cell number	Net O_2 Production as carbon[a] ÷1.25	PQ = O_2/CO_2[c]
Dunaliella tertiolecta							
1	–	0.93	–	0.93	–	1.30	1.65
2	–	1.45	–	1.45	–	2.32	1.89
3	1.70	1.77	1.72	1.73	1.60	1.94	1.37
4	1.83	1.79	1.89	1.84	1.34	1.69	1.16
5a 0.14 ly/min	–	3.53	–	3.53	–	–	–
5b 0.035 ly/min		1.53	–	1.35	–	–	–
Skeletonema costatum							
1	0.36	0.46	0.45	0.42	0.11	0.64	1.8
2	3.2	3.15	3.50	3.28	4.1	4.53	1.78
3(NH_4)	–	0.88	0.91	0.90	0.90	1.28	1.7
4(NH_4)	–	1.32	–	1.32	–	1.57	1.49
Ditylum brightwellii							
1	1.4	0.98	0.97	1.12	0.80	1.51	1.49
2	1.59	1.62	1.60	1.60	1.63	1.85	1.62
Thalassiosira rotula	2.08	1.97	1.57	1.87	2.30	2.50	1.69
Cyclotella nana	0.69	0.65	0.75	0.70	0.54	0.79	1.5
Red tide							
1	–	4.31	–	4.31	–	2.97	0.89
2	2.00	2.13	2.06	2.06	–	2.58	0.98
Peridinium trochoideum	–	0.63	0.64	0.64	0.53	0.57	1.1
Coccolithus huxleyi	0.77	0.54[d]	0.92	0.72	–	0.69	1.2
Syracosphaera elongata	3.3	3.1[e]	2.9	3.1	–	3.84	1.6

[a]Corrected for median excretion value.
[b]Mean of columns 1, 2, and 3.
[c]Mean net C-assimilation + excretion.
[d]No coccoliths present.
[e]Coccolith C^{14} increase 0.3 mg C/litre. Total C^{14} assimilations 3.4 mg C/litre.

TABLE III. Summary of data for the excretion of dissolved organic carbon (in milligrams/litre).

Experiment/Method	(1) C^{14} filtrate	(2) Dissolved oxidizable organic-C	(3) Dissolved CO_2 less net assimilation	(4) Median of (1), (2), and (3)	(5) Net O_2 production as carbon less mean net carbon assimilation[a]
Dunaliella tertiolecta					
1	0.13			0.13	0.50
2	0.22			0.22	1.09
3	0.24		0.3	0.27	0.44
4	0.38		0.4	0.39	0.22
5a 0.14 ly/min	0.50			0.50	
5b 0.035 ly/min	0.18			0.18	
Skeletonema costatum					
1	0.03		0.0	0.03	0.23
2	0.04	0.0	0.3	0.04	1.32
3(NH_4)	0.25	0.6	0.3	0.3	0.70
4(NH_4)	0.01			.01	
Ditylum brightwellii					
1	0.16	0.6	0.6	0.6	0.93
2	0.25	0.0	0.0	0.0	0.23
Thalassiosira rotula	0.33	0.5	0.0	0.33	0.86
Cyclotella nana	0.03	0.0		0.03	0.17
Red tide					
1	0.09			0.09	−0.48
2	–		1.2	1.2	0.45
Peridinium trochoideum	0.07	0.1	0.0	0.07	0.01
Coccolithus huxleyi	0.01	0.0	0.2	0.01	0.16
Syracosphaera elongata	0.05		0.0	0.05	1.4

[a] Oxygen production ÷ 1.25.

included for comparison only. Even the other three methods give poor agreement in most cases.

Because none of these estimates of excretion can be used conveniently at sea we sought other ways of predicting excretion. Our only success has been

in comparing net assimilation rate per unit chlorophyll *a* between experiments (Fig. 1). The average rate was 2.8 mg C/mg chl *a* · hr; in experiments *Ditylum* 1 and *Skeletonema* 3 net assimilation/chl *a* · hr was low. The difference between these rates and the average seems to be related to the magnitude of excretion (Fig. 1). This relationship contrasts with that for *Dunaliella* which excretes a constant fraction of photosynthetic product regardless of conditions (Fig. 1). *Thalassiosira rotula* excreted the same amount of carbon in light and dark.

Conditions Favouring Excretion

We have not made a systematic study of factors influencing excretion but only some miscellaneous observations. Hellebust (1965) has found that a number of substances is excreted by phytoplankton. *Dunaliella tertiolecta* excretes glycerol primarily (Hellebust, 1965; Craigie and McLachlan, 1964). In the dark we find that about 70% of the excreted material (glycerol) is reabsorbed within an hour by this organism (Fig. 2). A similar decline in the quantity of excreted material in the red tide population may be due to heter-

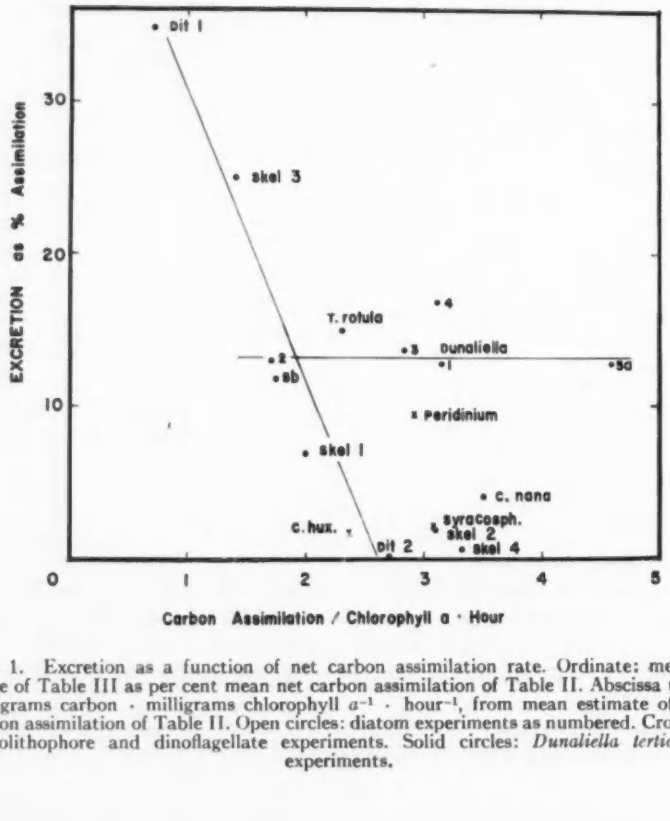

Fig. 1. Excretion as a function of net carbon assimilation rate. Ordinate: median value of Table III as per cent mean net carbon assimilation of Table II. Abscissa units milligrams carbon · milligrams chlorophyll a^{-1} · hour^{-1}, from mean estimate of net carbon assimilation of Table II. Open circles: diatom experiments as numbered. Crosses: coccolithophore and dinoflagellate experiments. Solid circles: *Dunaliella tertiolecta* experiments.

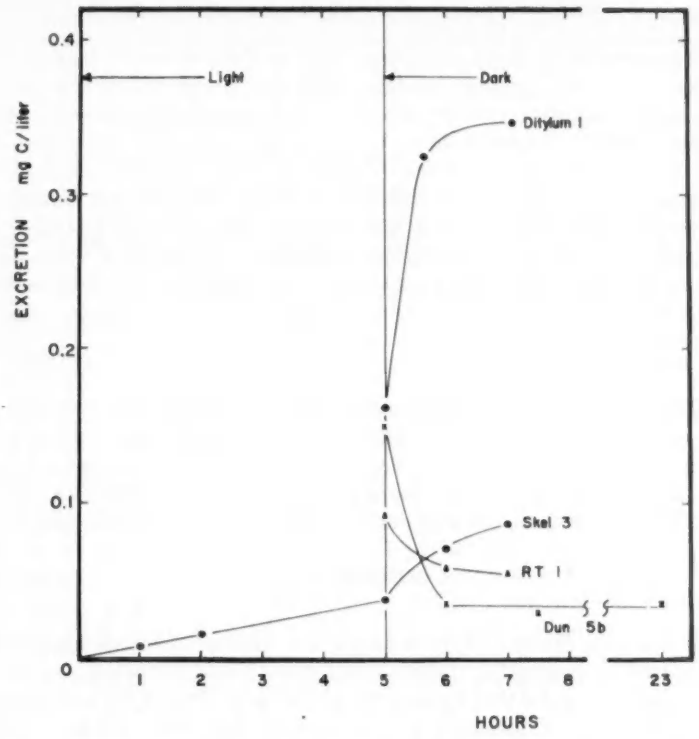

FIG. 2. Time course of excretion as estimated by carbon[14] of culture filtrates (RT 1 = red tide experiment 1, Dun. 5b = *Dunaliella tertiolecta* experiment 5b, etc.).

otrophs present in the population. Curiously, both *Skeletonema* and *Ditylum* showed increased excretion in the first hours of darkness. This may be a transient effect but we cannot be certain because dark incubations were continued only 2 hr.

Excretion is well known in free-living freshwater Chlorophyta as cultures approach senescence. This effect may be responsible for the extensive excretion in *Ditylum* (experiment 1) and *Skeletonema* (experiment 3). In both cases net assimilation/chlorophyll *a* · hour and growth rate had declined by the time the 5-hr experimental incubation was commenced. Likewise the ratio net assimilation/respiration, (P/R), which declines in nutrient deficiency (Ryther, 1954; Thomas, 1963), seems to correlate both to high culture density and low photosynthesis/chlorophyll *a* · hour, and is low when excretion is pronounced.

However, some species (*Dunaliella* and possibly *Thalassiosira* in this study) excrete even during exponential growth.

Respiration

We considered it likely that these phytoplankton would display a light-enhanced respiration greater than that indicated by dark-bottle oxygen consumption. We sought to measure this effect in *Dunaliella*, *Skeletonema*, *Ditylum*, *Coccolithus*, and in the red tide experiments by noting the loss of cell radiocarbon in the dark after the light incubation. Only *Dunaliella* showed a rate of carbon loss exceeding that predicted by dark-bottle oxygen consumption. We have concluded, lacking mass spectrometer data, that dark-bottle oxygen consumption (Table IV) is a reliable estimate of respiration over the 5-hr experiments carried out. Loss of particulate cell carbon in dark bottles was too small for accurate measurement and the data are not reported.

Gross Photosynthesis

Values in Table IV, column 5, are the algebraic sums of the mean estimates of net assimilation, the median estimates of excretion, and the dark-bottle respiration (summation estimate). For *Dunaliella* only we include a respiration rate obtained from the rate of loss of cell radiocarbon in the dark. An independent estimate of gross photosynthesis is derived from oxygen data.

DISCUSSION

Reliability of Methods

The precision realized in determining net carbon assimilation is probably best indicated by comparing the deviation of each analysis of each experiment from the mean value for that experiment of Table II. *Dunaliella* experiments 1, 2, and 5, *Skeletonema* 4, and red tide 1 are excluded from the calculation because cell carbon and dissolved CO_2 determinations were not successful (Table V). Estimates of net assimilation were computed also from chlorophyll *a* and carotenoid increase assuming cell composition to be constant. Variability in chlorophyll *a* estimates was less than that from O_2 production less excretion. Carotenoid estimates gave greater variability. Neither gave an efficient estimate of net assimilation in the sense of being generally close to the mean value of the cell carbon, cell C^{14}, and dissolved CO_2-less excretion estimates.

The C^{14} productivity method for field work is considered to have a greater error (7–13%) than we find in the laboratory (Thomas, 1963). Part of this must be due to standardization of C^{14} in ampules and uncertainty in determining G-M counting efficiencies for cells on filter pads. The C^{14}/C^{12} discrimination factor of 1.05 or 1.06 (Steeman Nielsen, 1955) seems to be correct and appropriate from our data.

Organic radiocarbon in filtrates gave the most sensitive estimates of excretion. However, we suspect that certain of these determinations gave low values due to the volatility in acid of excreted compounds, or because the specific activity of excreted carbon is less than the carbon recently assimilated. Some excreted carbon may come from previous nonlabelled products of photosynthesis. This is suggested by the equal excretion of *Thalassiosira* in

TABLE IV. Estimates of gross photosynthesis and respiration.

	As mg C/litre per 5-hr experiment					
	Respiration				Gross photosynthesis	
	(1)[a]	(2)	(3)	(4)	(5)	(6)
Experiment/Method	DB O_2 consumption	Dark C^{14} loss	Net O_2 production as carbon[b]	Gross O_2 production as carbon[c]	Mean net C-assimilation + excretion + respiration	Mean net C-assimilation + excretion + dark C^{14} loss
Dunaliella tertiolecta						
1	0.21	0.59	1.43	1.64	1.39	1.67
2	0.40	1.18	2.54	2.94	2.08	2.86
3	0.38	0.81	2.22	2.60	2.40	2.83
4	0.21	1.02	2.23	2.44	2.42	3.33
Skeletonema costatum						
1	0.19		0.67	0.86	0.66	
2	0.49		4.57	5.06	3.8	
3 (NH_4)	0.52		1.57	2.09	1.7	
4 (NH_4)	0.50		1.97	2.47	1.83	
Ditylum brightwellii						
1	0.80		1.91	2.71	2.4	
2	0.25		1.84	2.09	1.85	
Thalassiosira rotula	0.39		2.83	3.22	2.48	
Cyclotella nana	0.14		0.82	0.96	0.82	
Red tide						
1	0.90		3.06	3.96	4.47	
2	0.17		2.58	2.75	2.3	
Peridinium trochoideum	0.39		0.64	1.03	1.10	
Coccolithus huxleyi	0.44		0.70	1.14	1.2	
Syracosphaera elongata	0.74		3.89	4.63	3.8	

[a] RQ = 1.0.
[b] PQ = 1.25.
[c] From PQ = 1.25, RQ = 1.0.

TABLE V. Precision in determination of net carbon assimilation.

Method	Average deviation of each value from mean value of Table II, column 4	Range of deviations	No. experiments
	%	%	
Cell carbon	+ 1.9	−14 to +20	11
Cell C^{14}	− 1.8	−19.5 to + 9.5	13
Dissolved CO_2 less excretion	+ 1.1	−16 to +28	13
Cell number	−14	−74 to +25	9
Net O_2 production + 1.25 less excretion	+23	− 4 to +52	13

light and dark, as measured by dissolved organic carbon increase and by the enhanced excretion of *Skeletonema* and *Ditylum* of C^{14}-labelled organic matter in the dark (Fig. 2). Increase in dissolved, oxidizable organic carbon was determined with a precision of about ±0.2 mg C/litre. The difference between the decrease in dissolved CO_2 and mean net assimiliation, as an estimate of excretion, gives a calculated precision of about ±0.25 mg C/litre, and thus will only indicate excretion when it is relatively high. We conclude that our estimates of excretion are at best only semi-quantitative.

RELATIONSHIPS AMONG THE MEASUREMENTS

Steemann Nielsen (1955), Ryther (1954), and Thomas (1963) discuss computing gross photosynthesis from C^{14} assimilation × F, where F varies with the nutritional status or otherwise past history of the cells. Values of F computed from our summation estimate of gross photosynthesis agree precisely with Ryther's *Dunaliella* values in their variation with the ratios of photosynthesis/respiration (P/R). Steemann Nielsen's values (from *Chlorella*) are higher.

The linear relationship between the ratios of net/gross photosynthesis and chlorophyll *a*/carotenoid found by Ketchum *et al.* (see Yentsch, 1962) for nutrient deficient *Dunaliella* does not hold for our data either from (presumably) nutritionally healthy cells or from cells in incipient senescence.

The close correspondence between estimates of net assimilation from cell carbon increase, cell number increase, decrease in dissolved CO_2 less excretion, and particulate C^{14} confirm the contention that the C^{14} productivity method gives a reliable estimate of net production defined as increase in phytoplankton cell carbon. Time course measurements of C^{14} assimilation failed to show transient rate changes observed by McAllister *et al.* (1964) in *Dunaliella* and *Skeletonema*. We observed a steadily increasing rate with time, correponding

to growth. We attribute the transient changes of McAllister *et al.* to the use of different intensities of light during measurement than prevailed in preculture. We did observe the effect with *Dunaliella* when the experimental light intensity was one-half the culture intensity.

Excretion

The magnitude of excretion in the diatoms studied is related to low P/R values, low ratios of photosynthesis/chlorophyll *a* (Fig. 1), and to declining growth rates. All these measures of physiological activity are complex, unfortunately, and reflect at least past light exposure, temperature, age of the culture, and nutritional status, but they can serve as an index of physiological activity of cells. With the exception of *Dunaliella*, and possibly *Thalassiosira rotula*, excretion is inversely proportional to physiological activity. These exceptions point out the probability that excretion, in the sense used here, may result from different mechanisms.

Photosynthetic Quotient

Myers and Cramer (1948) noted that the PQ in *Chlorella* varies with the intensity of illumination at measurement. Shade cells measured at high intensities gave lower PQs than the same cells measured at low intensities. The same relationship is apparent for *Dunaliella tertiolecta* in fig. 6 and 7 of McAllister *et al.* (1964) and may explain the variation in the PQ we note with this organism. While incident intensity was nominally constant throughout, mutual shading in denser cultures reduced the average intensity seen by each cell. For experiments *Dunaliella* 1–4 we calculate this average intensity per cell (by dividing incident light intensity by cell concentration) to be relatively 63, 50, 80, and 82 corresponding to PQs of 1.65, 1.89, 1.37, and 1.16, respectively. PQ seems to vary with average intensity per cell in *Dunaliella*.

Thomas (1963) noted a high PQ for *Dunaliella primolecta* cultures in phosphorus deficiency. McAllister *et al.* (1964) show this also for P-deficient *D. tertiolecta* and for *Skeletonema* deficient in both N and P. We have no reason to believe nutrient deficiency to be the cause of the high PQ we observed in diatoms except perhaps in experiment *Ditylum* 1.

Changing the N-source from NO_3 to NH_4 with *Skeletonema* reduced the PQ from about 1.8 to about 1.6 but this is still far higher than the expected value. We postulated that NO_3 might be reduced to NH_4^+ which was then excreted and we tested this idea in experiment *Skeletonema* 2 but found only enough NH_4^+ released to the medium to account for 1% of the PQ discrepancy.

Because anticipated PQ values were found with dinoflagellates and *Coccolithus huxleyi* we think that our measurements are valid and that the high PQs for diatoms are real. Consideration of average light intensity per cell was not helpful as it was with the *Dunaliella* experiments nor did PQ correlate with pH. McAllister *et al.* (1964) considered the PQ for *Skeletonema* to be too high to be explained by any mechanism other than the excretion of organic matter.

We find high PQ values to be independent of excretion by direct measurement. It is apparent that either we are pursuing an artifact or that these marine diatoms have an unusual metabolic feature in their excess oxygen production.

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NOTES

Preliminary Results on the Seasonal Size Distribution of *Mytilicola orientalis* and the Effect of this Parasite on the Condition of the Pacific Oyster, *Crassostrea gigas*[1,2]

Five experimental sites were established in March 1963 to study the seasonal size distribution of *Mytilicola* and the effects of this parasite on the condition of Pacific oysters (*Crassostrea gigas*). One station was situated in Humboldt Bay, California, another in Yaquina Bay, Oregon, and three in Washington State, located in Hood Canal, Oyster Bay, and Willapa Bay. Oysters were placed in baskets on a float at all stations and, with the exception of Yaquina Bay, oysters in baskets were tied to a rack on the beds. Sampling was made every 2–3 weeks.

To document the original infection rates of various shellfish populations at the beginning of the study, samples of Pacific oysters used in this investigation were preserved for copepod counts during February 1963. The highest infection rate (32.9%) occurred at Yaquina Bay and the lowest rate occurred in Oyster Bay (1.0%), with Humboldt Bay falling between (14.1%). The oysters in the Washington stations remained at a low level of infection through the second summer, but the Humboldt Bay and Yaquina Bay oysters maintained their heavy infections by *Mytilicola*. Oyster Bay is representative of all three Washington stations since it was the original source of populations for the other two stations.

Two distinct size classes of *M. orientalis* were found throughout the year for the Humboldt Bay and Yaquina Bay oysters. Those between 2 and 5 mm were observed to be mostly males, with a few immature females noted in the 4–5-mm range throughout the year. It is difficult at this time to assess whether the 2–3-mm males were mature, since no histological examinations were made and no information is available on the life history of this species of copepod. Those copepods found between 6 and 11 mm were females. Throughout the sampling, all of the females of approximately 6 and 7 mm were either mature with well-developed egg cases, or immature females well along in development but without visible egg cases. Some of the larger females (8–10 mm) in the samples were noted to have either undeveloped egg cases, or developed cases which were sloughed or broken off after the eggs were hatched.

It has generally been found by researchers that the presence of *Mytilicola* in the intestinal tract of bivalves brings about lower condition index (C.I.) values (Odlaug, 1946; Cole and Savage, 1951; Korringa, 1951). Relative to

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this assumption, Table I presents a summary of infection rates and the relation of the infection rate with modified C.I. The modified C.I. was taken for each oyster collected and was expressed as the ratio of the wet weight of the meat (in grams) to the volume of shell cavity (in cubic centimeters) multiplied by 100. As shown in Table I, those oysters with below average C.I., with the exception of Oyster Bay which had very low infections, had significantly higher percentages of infections. This was confirmed by chi-square analysis of the data. Also, in those areas (Humboldt Bay, Yaquina Bay, and Willapa Bay) where the numbers of *Mytilicola* were high enough to warrant computations of the average number per infected oyster, the average number of parasites per infected oyster was significantly higher in the below average C.I. group than in the infected oysters with above average C.I. (Table I). Analysis of variance test supports this finding.

The levels of infection by *Mytilicola* encountered throughout the study did not appear to affect the overall dimensional growth of oysters, since the growth curves of Pacific oysters in Humboldt Bay and Yaquina Bay were not interrupted during or after the time when higher infections occurred.

The two areas of heaviest infection (Humboldt Bay and Yaquina Bay) were observed to have the highest and lowest overall *C. gigas* mortalities. Between March 1963 and May 1964 Humboldt Bay float and intertidal rack

TABLE I. Summary of *Mytilicola* infection rates in Pacific oysters (*Crassostrea gigas*) which were individually conducted for modified condition index (C.I.) (March 1963 through May 1964).

	Per cent infection		Average no. *Mytilicola* per infected oyster	
	Above average C.I.	Below average C.I.	Above average C.I.	Below average C.I.
Humboldt Bay	16.6% (67 out of 403 infected)	28.5% (122 out of 428 infected)	3.1	5.2
Yaquina Bay	29.2% (79 out of 271 infected)	38.2% (120 out of 314 infected)	2.9	4.0
Willapa Bay	9.5% (27 out of 285 infected)	17.2% (43 out of 250 infected)	2.4	6.7
Oyster Bay	3.5% (8 out of 228 infected)	3.8% (9 out of 236 infected)	–[a]	–
Hood Canal	5.4% (14 out of 260 infected)	10.9% (29 out of 265 infected)	–	–

[a]Computations were not made due to low infections and low numbers of copepods encountered.

oysters had 13.7% and 15.4% cumulative mortalities, respectively, and Yaquina Bay float oysters had only 1.0% with the Washington stations intermediate. Unfortunately, comparison of oyster mortalities in the float with those in the intertidal rack was impossible for Yaquina Bay due to there being no suitable intertidal location.

Of particular interest was the fact that 10.0–11.0% of the cumulative mortalities for Humboldt Bay occurred between July and October 1963. Preliminary histological examination of live and gaping (dying) oysters in Humboldt Bay during this period revealed heavy infections of an unidentified microorganism in the tissues. Further work is presently being conducted to identify this organism, which is suspected of causing the higher mortalities in Humboldt Bay.

Despite the extensive tissue damage reported by Sparks (1962) with infections of *M. orientalis*, no apparent relationship exists between infection of *C. gigas* by *Mytilicola* and mortality. Infection levels were higher during the summer months in Humboldt Bay at a time of peak mortality. However, cumulative mortality rates in Yaquina Bay remained at only 1% during a time of similarly high infections.

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Predation on Lobsters (*Homarus americanus*) by *Anonyx* sp. (Crustacea, Amphipoda)

On January 27, 1965, about 1 dozen lobsters were received from Grand Manan, New Brunswick. Without exception these lobsters were fresh; all, however, had had the soft parts wholly or partly consumed by amphipods (Fig. 1). These lobsters were part of a consignment of freshly-caught, live lobsters that had been loaded into crates the previous evening and left floating overnight in Seal Cove, Grand Manan. In the morning they were hauled out of the water prior to shipping. It was then that the amphipods were first noticed, although the extent of the damage was not established until several hours later when the crates were unpacked at their destination. A total of about 50 lb of lobsters out of a consignment of 800 lb had been damaged. This was a higher mortality than would normally be expected over such a short period. In most carcasses the vent had been eaten away, and also thin areas of membrane on the ventral surface near the origin of the appendages (Fig. 2, 3). There was a report of some lobsters still showing signs of life while partly consumed by amphipods. This, together with the high mortality, suggests predation rather than scavenging.

Several amphipods were removed from the lobsters and tentatively identified as *Anonyx nugax* Phipps (Sars, 1895). Bousfield (1962) has recorded this species from Passamaquoddy Bay.

Dr E. L. Bousfield, National Museum of Canada, Ottawa, and Mr Pierre Brunel, Station de Biologie Marine, Grande-Rivière, recently identified this amphipod as an undescribed species of *Anonyx*, endemic to American-Atlantic coastal waters, closely related to *A. nugax* Phipps. Mr Brunel, in collaboration with Dr D. H. Steele, Memorial University, St. John's, is currently revising the genus *Anonyx* in the northwestern Atlantic region, but the species' definitions and new nomenclature have not yet been prepared for publication.

The Grand Manan specimens of *Anonyx* reach 23 mm in length. In colour they are creamy and may display a pale purplish stripe on each side. The eyes are black.

Hart (1942) recorded *A. nugax* attacking and consuming herring and cod held in live boxes at Burgoyne Bay, British Columbia. These occurrences also were in January, although by the end of February the amphipods failed to appear when bait was put out for them.

Several live specimens of *Anonyx* sp. were placed in an aquarium with a vigorous, 1-lb lobster. They swam around the tank and each time one touched the lobster it reacted, brushing the amphipod away or flipping its tail violently. Occasionally the lobster caught and ate one of the amphipods and after 6 hr about a dozen had been consumed. The temperature of the water was 2.5 C. It would appear that healthy lobsters are able to resist attack by amphipods

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except in situations where movement is restricted such as when packed in a lobster crate.

Previous records of predation upon lobsters by amphipods concern the amphipod *Orchomenella pinguis* (Templeman, 1954, 1958). *Orchomenella pinguis* is sometimes abundant in the Bay of Fundy during late summer and fall and is well known by fishermen to eat both lobsters and lobster bait. This species is much smaller (7 mm), white, and has red eyes.

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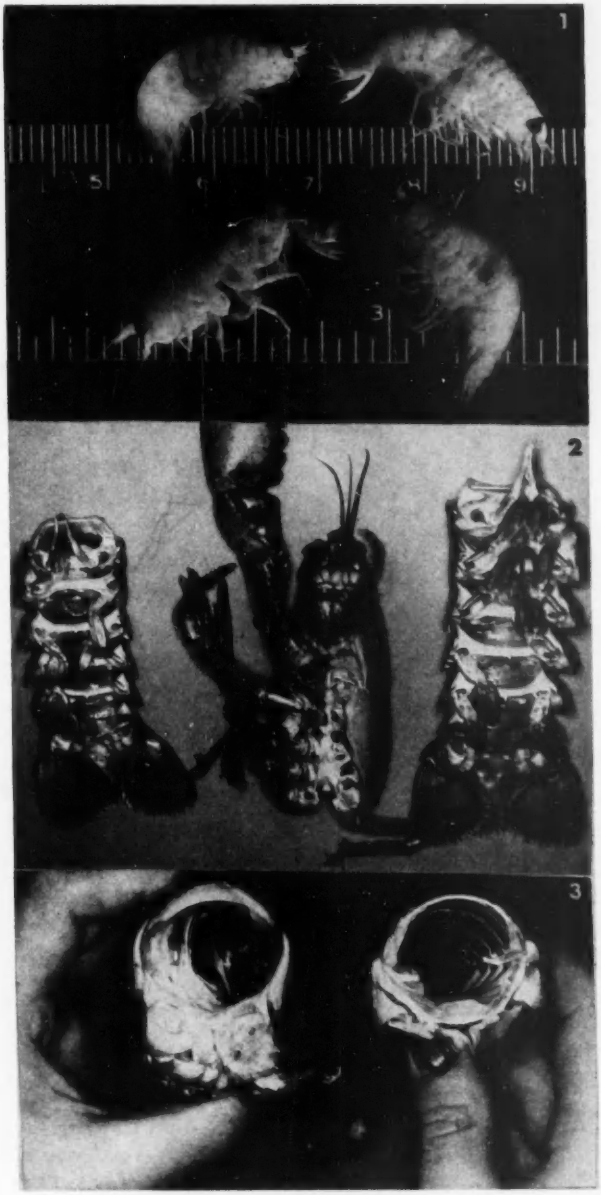

FIG. 1. *Anonyx* sp. Two male and two female specimens. The males have longer antennae and larger eyes. (Upper scale, centimetres; lower scale, inches.)

FIG. 2. Portions of lobster carcasses after predation by *Anonyx* sp. showing the vents and soft membranous parts eaten away.

FIG. 3. View into the body and tail of a lobster eaten by *Anonyx* sp. The soft parts had been entirely consumed.

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